DO THE SUBJECTIVE VISUAL VERTICAL AND THE SUBJECTIVE HAPTIC VERTICAL PROBE A COMMON ESTIMATE OF GRAVITATIONAL UPRIGHT?

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Abstract

In the subjective visual vertical (SVV) and the subjective haptic vertical (SHV) task, participants must judge the alignment of a probe rod with perceived gravitational vertical by sight or by touch. Previous research suggests that as the body is roll-tilted, SVV and SHV show a systematic, distinct pattern of errors, although reports vary. The purpose of this research was to identify whether SVV and SHV probe the same underlying representation of gravity. In Experiment 1, I confirmed that SVV and SHV errors are divergent by comparing the two measures in the same participants. In Experiment 2, I varied the tilt of the head and body separately and applied galvanic vestibular stimulation to introduce vestibular noise. I found these manipulations had differential effects on SVV and SHV. Experiment 3 showed that when neck afferents were stimulated, SVV and SHV integrate optimally, pointing to two distinct underlying estimates of gravity vertical.

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List of Acronyms

ADJ	**-**	Adjustment
FR	**-**	Forced Response
GVS	**-**	Galvanic vestibular stimulation
MLE	**-**	Maximum Likelihood Estimate
OCR	**-**	Ocular counterroll
PSE	**-**	Point of Subjective Equality
PSI	**-**	psi-method adaptive staircase procedure
QUEST-		QUEST adaptive staircase procedure
SD	**-**	Standard deviation
SHV	**-**	Subjective haptic vertical
SVV	**-**	Subjective visual vertical

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CHAPTER1: Introduction

1.1 Overview

In order to move, maintain balance and complete a myriad of everyday behaviours, we must be able to reliably detect the direction of gravity as it acts on ourselves and on the world. Sensory cues to the direction of gravity include those from the vestibular system, somatosensation, 'somatic graviception' and vision. A number of psychophysical paradigms have been developed to try and measure our subjective perception of gravity, especially in the absence of visual cues to "up." The subjective visual vertical (SVV) and the subjective haptic vertical (SHV) are both intended to probe an underlying percept of gravity by asking participants to position a visual or tactile stimulus so that it is aligned with gravity vertical. Previous research shows that the SVV becomes biased when participants are laterally tilted (rolled). The SHV also shows a bias that appears distinct from the pattern of SVV errors, but potential experimental confounds and the variability in reported errors makes it difficult to contrast the two. The goal of this thesis is to clarify the relationship between SVV and SHV as measures of perceived vertical, and their connection to underlying mechanisms of gravity perception. In addressing this topic I hope to elucidate some of the underlying causes of SVV and SHV errors.

In Chapter 2, I compare both SVV and SHV measures in the same participants over a range of roll tilts, using a more robust testing methodology than that of previous research. Thus I highlight the differences between the two measures, and replicate previous SVV and SHV findings in the same subject group. In addition I introduce a novel bimodal measure of vertical to explore how visual and haptic sensory estimates might integrate in a single measure. In Chapter 3, I isolate head and body tilt and their effects on SVV and SHV, and add noise to the vestibular system using galvanic vestibular stimulation. Thus I identify the relative contribution of different body parts, and of the vestibular system, to SVV and SHV. In Chapter 4, I explore the ability to optimally integrate visual and haptic estimates of an object's alignment with gravity vertical (e.g., its verticality), as a means of exposing the underlying structure of the estimate(s) of the gravity vector accessed by both tasks.

1.2 Sensory information about gravity

The vestibular system of the inner ear, in particular the utricle and saccule (collectively known as the otolith organs) have evolved to detect linear acceleration and the position of the head relative to gravity vertical. These organs are small sacs that contain a patch of sensory cells on the interior membrane known as the macula. Each macula is roughly 2mm in diameter and composed of sensory hair cells and supporting cells, a base membrane through which cells connect to nerve fibers leading to the brain, and connective tissue (see Figure 1.1). The sensory hair cells project up into a gelatinous matrix, on top of which rests calcite crystals (the otoliths). Changes in movement are detected when inertia causes the much denser otoliths to shear over the matrix, bending the embedded hair cells and causing them to fire. This sensory signal is carried along the connected nerve fibres in the base layer of the membrane to the brain. When the head is stationary in a given position, gravity's constant linear acceleration acts on the otoliths and provides the brain with information about the position of the head with respect to gravity (Böhmer & Mast, 1999; Hess, 2001).

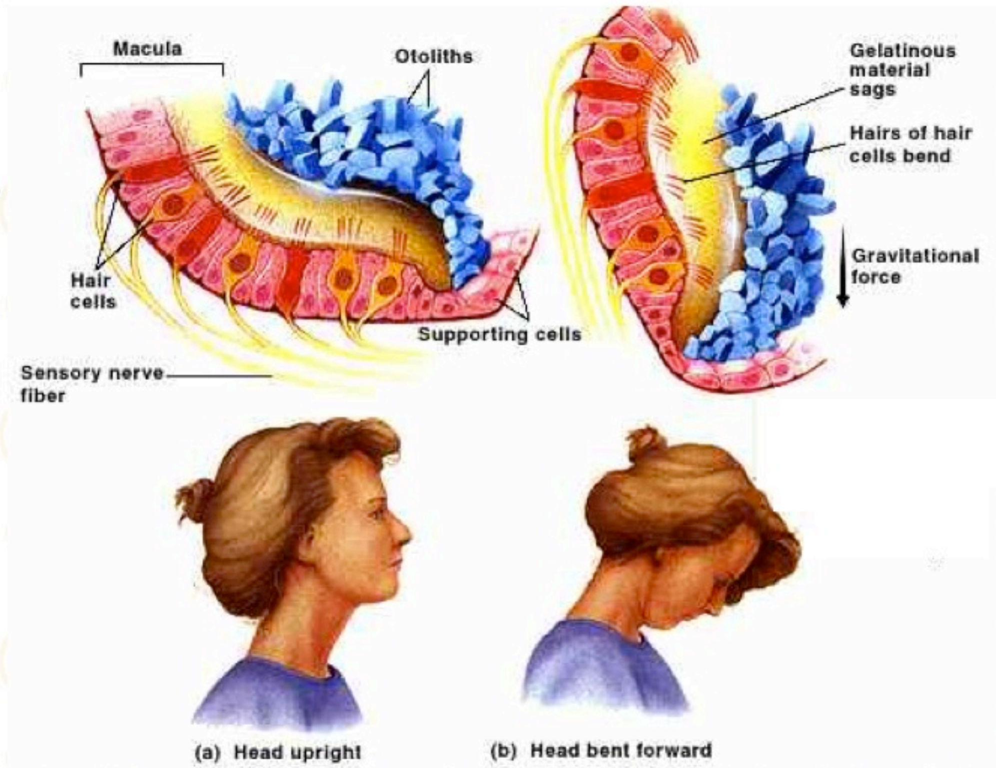


Figure 1.1. Illustration of how the utricle (positioned roughly horizontally) is sensitive to the direction of gravity in different head positions. From Shier et al., 1996.

Additional sensory information about the direction of gravity is provided by somatosensory and proprioceptive cues, for example pressure cues on the feet (when standing), bottom (when sitting) or trunk (when lying or leaning in a chair), and the perceived orientation of the neck (Clemens et al., 2011). In addition, there are 'somatic graviceptive' cues originating from sensors around the kidneys (Mittelstaedt,1997; Trousselard et al., 2004). Collectively, these cues provide information concerning gravity's direction with respect to the self, that is, they are *egocentric* cues to gravity. We also have *allocentric* cues to gravity from vision that tell us about gravity's direction with respect to the external world (e.g., a horizon, objects resting on other objects, etc; Asch & Witkin, 1948; Witkin, 1949; Dyde et al., 2009). When few cues to an allocentric gravity vector are available (i.e., in a dark room), we likely encode both the perceived direction of gravity and the object's orientation in an egocentric (self based) coordinate system and compare the two within this frame of reference (Mittelstaedt, 1983).

The subjective perception an object's orientation with respect to gravity is known as its subjective verticality. Two psychophysical methods of testing the accuracy and precision of subjective verticality are the subjective visual vertical (SVV) and the subjective haptic vertical (SHV).

1.3 The subjective visual vertical

The subjective visual vertical (SVV) is a psychophysical paradigm that assesses perceived object alignment with respect to gravity vertical (i.e., its "verticality"). In the "adjustment" version of the SVV paradigm (henceforth ADJ), participants are presented with a luminous line and must adjust the orientation of the stimulus so that it is aligned with the perceived direction of gravity, using a verbal command, mouse, joystick or other apparatus. In the "forced-response" version (henceforth FR, not to be confused with a 2AFC task, which presents participants with two stimuli), participants view a sequence of tilted lines and must respond whether each line is tilted to the left or right of gravity vertical. These responses can then be plotted and fitted with a psychometric function, to determine the stimulus orientation at which participants respond with either 'left' or 'right' with an equal likelihood. This is known as the Point of Subjective Equality (PSE), and is taken as the perceived orientation of gravity vertical. Baccini and colleagues (2013) compared the ADJ and FR approaches to the SVV task and found they produce equivalent results, however, the FR task proved to be more robust against response artifacts.

When standing upright, participants' SVVs are accurate within ± 2° (Friedmann, 1970; Howard, 1982). However, at small roll tilts of 30°-60° (see Figure 1.2 for examples of yaw, pitch and roll tilts), researchers report small biases in perceived verticality away from true vertical in the direction of tilt (Ceyte et al., 2009; Barra et al., 2010; Wade & Curthoys, 1997; Van Beuzekom & Van Gisbergen, 2000; De Vrijer et al., 2004; Tarnutzer at al., 2009b). This phenomenon is known as the "A effect," after Hermann Aubert, who first reported the phenomenon in 1861 (Aubert, 1861).

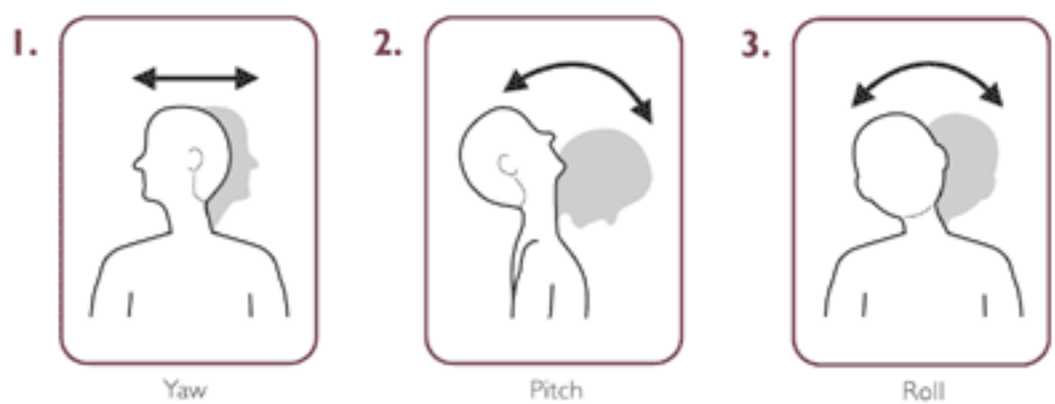


Figure 1.2. Examples of yaw, pitch and roll movements of the head. Taken from resourcesonbalance.com (accessed July 2014).

Conversely, some researchers have reported a bias in perceived verticality in the direction *opposite* body tilt (Wade, 1968; Betts & Curthoys, 1998; Clemens et al., 2011).

This phenomenon is known as the “E effect”, short for *entgegengesetzt*, which is German for ‘opposite,’ named by G. T. Müller in 1916 (Müller, 1916). Finally, some researchers have reported that in fact participants are accurate for roll tilts in the range of 30°-45° (McKenna et al., 2004; Tarnutzer et al., 2012; however it should be noted that these particular studies only manipulated the roll position of the head, and kept the body positioned upright). This variability in the literature may be due in part to the prevailing use of the ADJ method, as well as differences in the experimental task and the instructions used. The results of Experiment 3 (reported in chapter 4) also point to the possibility that the specific nature of the visual stimuli used could play a role whether an A or an E effect is found.

Guerraz and colleagues (1998) and Tarnutzer and colleagues (2010) have shown that the primary contributor to the errors in SVV is the roll position of the head, while the orientation of the trunk plays a secondary role. This is consistent with research showing a limited to negligible influence on these errors by somatosensation (largely a body-based signal), as evidenced by SVV measured underwater, which shows no difference in errors compared to on-land controls (Jarchow & Mast, 1999; Jarchow & Mast, 1996) and by ‘somatic graviception’ around the kidneys (also body-based) (Trousselard et al, 2004).

There are two theories for the source of A and E errors that cohere with a head-based source of error: a failure to compensate for ocular counteroll, a theory proposed and developed by Miller and Graybiel (1968); or a bias which shifts estimates towards the position of the longitudinal head and body axes, proposed by Mittelstaedt (1983) and further expressed as a prior by MacNeilage et al (2007).

When the head rolls laterally, the eyes counterroll in the opposite direction by roughly 10% of the tilt (Miller & Graybiel, 1962). Failure to account for this ocular counterroll (OCR) could generate an A effect by causing overestimation of the stimulus' tilt opposite the body's tilt, leading to a subsequent compensatory setting of the stimulus tilted towards the body. Significant correlations have been reported between SVV and OCR (DeGraaf et al., 1992; Wade & Curthoys, 1997). However, Miller and colleagues (1986) demonstrated that patients suffering bilateral vestibular loss had both decreased OCR activity and a marked exaggeration of the typical SVV error patterns, indicating that SVV and OCR are both driven by the otolith organs. Other researchers have found no correlation between the magnitude of OCR and SVV errors (Mast, 2000). Conflicting reports may be due in part to the difficulty associated with measuring the torsional position of the eyes.

Mittelstaedt (1983) has suggested that since adjusting a visual stimulus to align with the *head* position results in minor errors, it seems unlikely that OCR in general is uncompensated for in the SVV task. Thus, the source of error in the SVV task might stem not from perception of gravity or of the stimulus, but rather of the *comparison* of these two estimates in egocentric space.

Mittelstaedt proposed an influence of an "idiotropic vector," an internal bias towards the assumption that gravity vertical must be close to the longitudinal body axis (*idiotropic* means introspective, or towards the self). MacNeilage and colleagues (2007) modeled this vector as a Bayesian prior that shifts estimates of gravity vertical towards the head and body axes. Though the relative contributions of the head and body axes to this prior are somewhat unclear (this will be addressed in detail in chapter 3), the literature cited above seems to suggest that the head position is the more heavily weighted of the two components, at least for determining the SVV.

It has been argued that priors that modify sensory estimates become more heavily weighted relative to sensory information as sensory noise increases (e.g., MacNeilage et al., 2007). Sensory noise is reflected in the precision of internal estimates; the noisier the sensory cues driving the estimate, the less precise the estimate will be. In terms of the precision of SVV estimates, several studies have shown that trial-to-trial variability of ADJ responses increases as head tilt increases, peaking at about 120°-150° and then returning to intermediate levels when upside-down, thus yielding an m-shaped curve of variability over 360° of roll-tilt (Schoene & Udo de Haes, 1968; Udo de Hayes, 1970; De Vrijer et al., 2008). It has been suggested that this change in variability is due to the properties of the otoliths, which are not optimally tuned to detect tilts far from upright (Tarnutzer et al., 2009a; Jaeger et al., 2008). Thus we would predict a stronger bias in SVV at larger tilt magnitudes if a prior influences SVV estimates as it would be relatively more heavily weighted and pull the SVV towards the body axis; there is some empirical evidence for an m-shaped curve of the A effect (e.g., Betts & Curthoys, 1998; Barra et al., 2010), although this does not address the E effect sometimes found at small and very large roll-tilts (Kaptein & Van Gisbergen, 2004).

So, in summary, the SVV is thought to be a measure of the underlying perception of gravity. Systematic errors of visual verticality perception during roll have been reported; the variability of these reports makes it difficult to ascertain whether it the nature of these errors is visual (driven by OCR), or perhaps is separate from sensory information (an idiotropic vector or prior). Our understanding of gravity perception based on the SVV task remains unclear.

1.4 The subjective haptic vertical

Wade and Curthoys (1997) argued that the subjective visual vertical is confounded by the OCR and as such is a poor indicator of the true subjective perception of gravitational upright. These authors suggest that the subjective haptic vertical (SHV), a tactile judgment of a stimulus' verticality (i.e., its orientation with respect to gravity), avoids the torsional confound and thus provides an unqualified (i.e., non-confounded) measure of perceived vertical. Similar to the SVV, the SHV adjustment task asks participants to manually align a haptically felt rod to the perceived orientation of gravity. This is typically done in the absence of visual cues to the stimulus or the external world. Results of the ADJ method for SHV during lateral tilt show a distinctive pattern of errors compared to SVV, though, like the SVV, results are varied. Bauermeister and colleagues (1964) performed a comprehensive study on SHV using either one or both hands over a range of leftward and rightward whole body roll tilts. They found an E effect for the SHV that peaked at roughly 70° of tilt, with estimates of verticality shifting in the direction of the hand used (i.e., beyond the E effect, alignments made with the right hand were shifted right, left hand to the left, and alignments made with both hands were in the middle of single hand estimates). Schuler and colleagues (2010) reported similar findings of an E effect. In contrast, Bortolami et al. (2006a) reported an A effect for SHV at moderate lateral tilts. Tarnutzer and colleagues (2012a) tested head tilt only (with the body upright) and found participants' SHVs were accurate under this condition suggesting that head position may play less of a role in SHV than SVV.

While SHV estimates appear to differ from SVV estimates in nature, it is difficult to interpret the mixed results in the literature beyond this. One potential confound is that the ADJ method for assessing the SHV, as for all applications of ADJ methods, is sensitive to the effects of hysteresis (that is, the starting position of the test rod and hand influence the setting of its end position) (Tarnutzer et al., 2012b; Schuler et al., 2010). Thus, the characterization of SHV as an unqualified measure of perceived vertical may be somewhat premature.

To my knowledge, no one has previously used an FR method to probe the SHV. In Experiments 1 through 3, I implement the FR method for probing the SHV. I propose that, as with the SVV, an FR method is likely to be more robust against artifacts than the ADJ method for probing SHV. While using this method does not negate the effect of hysteresis entirely (as reach trajectory of the hand may still be a factor), I suggest that it minimizes some of the potential confounds associated with the ADJ method.

Finally, the role of the idiotropic prior proposed by Mittelstaedt (1983) in SHV judgments is still unclear, although Schuler et al., (2010) suggest the prior may be a purely visual phenomenon, which does not influence tactile judgments of verticality. The idiotropic prior and its relationship to the SHV task will be discussed further in Chapter 3.

Though the SHV paradigm avoids the potential confound of ocular torsion, it comes with its own limitations, and does not seem to provide a totally non-confounded measure of perceived vertical as has been suggested. The source of the distinct pattern of errors found in SHV compared to SVV is still an open question—whether it stems from modality-specific errors in object perception, and/or underlying differences in the nature of the two tasks, remains unclear. Without a direct comparison of the two techniques in an analogous testing paradigm that is robust against artifacts, it remains difficult to speculate on the relationship between these two tasks and the underlying perception of gravity they are thought to access.

1.5 The present research

This thesis presents three separate experiments aimed at elucidating the nature of SVV, SHV, and the underlying estimate(s) of gravity vertical that the two paradigms attempt to probe.

Experiment 1 is a direct comparison of the SVV and SHV at three levels of roll tilt (0°, 30° and 45°, left ear down) using a within-subjects experimental design, and the FR method. I hypothesize that increasing body tilt away from vertical will increase errors for both SVV and SHV, as has been previously reported. For SVV, I expect an A effect (underestimate of tilt) to emerge as degree of tilt increases, consistent with previous findings. Since no study to our knowledge has tested the FR version of SHV, I do not have a hypothesis for the SHV results; investigation of the directionality of SHV errors is exploratory in nature. In addition to testing SVV and SHV, Experiment 1 also introduces a novel bimodal probe as an exploration of the respective contributions of sight and touch to perceived object verticality within a single task. It is expected that this bimodal estimate will be an averaging of the SVV and SHV, implying integration of visual and haptic estimates (that may amount to an accurate verticality percept, if SVV and SHV err in opposite directions).

Experiment 2 draws on the findings of previous experiments that show head-only tilt can evoke SVV errors (e.g., Guerraz et al., 1998; Tarnutzer et al., 2010), while SHV appears to remain accurate under the same experimental conditions (Tarnutzer et al., 2012). I vary the tilt of the body and trunk separately (e.g., head-only tilt with body upright; body-only tilt with head upright) and measure the SVV and SHV in the same subjects, again using the FR method. In line with previous research, I expect that head-only tilt will evoke SVV errors, and body tilt may also evoke smaller SVV errors. In contrast, I hypothesize that body tilt will have a more pronounced effect on SHV than head tilt.

I also repeat the experiment with the addition of galvanic vestibular stimulation (GVS), to add noise to the vestibular signal. A noisier gravitational estimate should promote a stronger "idiotropic" prior that, if purely visual (as suggested by Schuler et al., 2010), would result in more pronounced SVV A effects, while not impacting SHV results.

Clemens et al. (2011) proposed a model in which either the head or the body can form the primary egocentric frame for gravity perception depending on the nature of the task. Experiment 3 revisits the bimodal task introduced in Experiment 1, and contrasts and compares two models of verticality perception: one proposed by Schuler et al., (2010) which states that SVV and SHV access the same underlying estimate of gravity, but modality-specific errors in object perception drive the differences in final estimates, and the one proposed by Clemens et al., (2011) which states that there are *two* underlying estimates of gravity, one head-based and one trunk-based, and that the SVV preferentially accesses the head-based estimate (I argue that SHV accesses the body-based estimate, which is a novel assertion). I therefore hypothesize that opposite errors in SVV and SHV may be due not only to modality-specific errors in object perception, but also to differences in the underlying gravity estimates used in the task. The bimodal probe developed in Experiment 1, by accessing both visual and haptic estimates, provides a unique window into the integration of these two estimates. Experiment 3 uses the principles of Maximum Likelihood Estimation to test the hypothesis that under normal circumstances, there is shared noise between SVV and SHV estimates, indicating a potential single underlying gravity estimate. In addition, Experiment 3 adds dorsal neck muscle vibration to the paradigm in order to disrupt proprioceptive information about the neck, which links head-based and body-based estimates of gravity in Clemens et al's model (2011). When this knowledge is degraded, I hypothesize that the SVV and SHV will be independent estimates. This therefore tests the hypothesis that a single underlying gravity estimate is accessed in both tasks.

CHAPTER 2: Comparing SVV, SHV and a bimodal measure of vertical in a forced-choice task

2.1 Introduction

Some researchers have proposed that SVV errors during roll tilt reflect the involvement of a Bayesian prior shifting perceived verticality towards the longitudinal axes of the head and trunk, while other suggest they are a result of misperceived eye torsion (see section 1.2). Because the ocular countertorsion reflex is triggered by the vestibular system, it is difficult to dissociate these two possibilities experimentally (Dieterich & Brandt, 1993).

Wade and Curthoys (1997) argue that the SHV paradigm overcomes the torsion confound and presents an unqualified measure of verticality. SHV also shows errors during roll tilt, but the results of different studies vary (see section 1.3). One potential reason for this variability is that the traditional adjustment technique used for SHV is sensitive to the effects of hysteresis (that is, the starting position of the test rod influences the setting of its end position) (Tarnutzer et al., 2012b; Schuler et al., 2010). Thus SVV and SHV results in the literature are not directly comparable.

This experiment seeks to directly compare SVV and SHV in the same subjects using a more robust testing method than the typically used adjustment paradigm. SVV and SHV will be tested in the same subjects under three (between-subjects) levels of whole-body tilt: upright, 30° left, and 45° left, using a forced-response paradigm (henceforth FR), where participants will be presented with a stimulus at a given orientation and will judge whether it is tilted to the left or right of the direction of gravity (either by sight or by touch). Baccini and colleagues (2013) report that for SVV, this method provides comparable results to the ADJ task, while being less sensitive to artifacts, and so I expect that SVV errors will mirror previous research showing a bias in SVV towards the body midline that becomes more pronounced as roll tilt increases (A effect). To my knowledge, no formal comparison has been made between an ADJ and FR for the SHV task, thus this experiment treats SHV as an exploratory measure, and no hypotheses have been made.

It is the goal of this study to clarify the relationship between SVV and SHV measures as groundwork for the investigation of differences in the nature of the two tasks. In addition to this comparison, I introduce a novel, bimodal measure of perceived verticality, in which participants use both sight and touch to assess object verticality. This measure is introduced in the interest of seeing whether simultaneous access to unimodal estimates might suppress or average modality-specific errors—in which case it may prove a more effective tool for measuring perceived vertical than either unimodal task.

2.2 Methods

2.2.1 Participants

Forty-eight participants (aged 18-27, 28 female and 20 male) took part in this experiment. Participants were all undergraduate students at York University; they received a 1% bonus credit towards their Introduction to Psychology course as compensation for participating. All participants had normal or corrected-to-normal visual acuity. Three of the participants identified themselves as left-handed. All experiments were approved by the ethics board of York University and were run according to the principles of the Declaration of Helsinki.

2.2.2 Apparatus

Platform

Participants stood or lay against a wooden platform set at one of three angles (0°, 30° left or 45° left), so that their body midline was upright or tilted in the roll plane, with the nose approximately 40 cm from the rotational center of a test rod. In the case of the tilted platforms a second board was attached perpendicularly at the base to support the participants' feet, and a stiff, square pillow was used to support the head and keep the head parallel to the board surface. An optional second pillow for the hips was provided for comfort. In the 0° condition participants were instructed to keep their head upright during the task (see Figure 2.1).

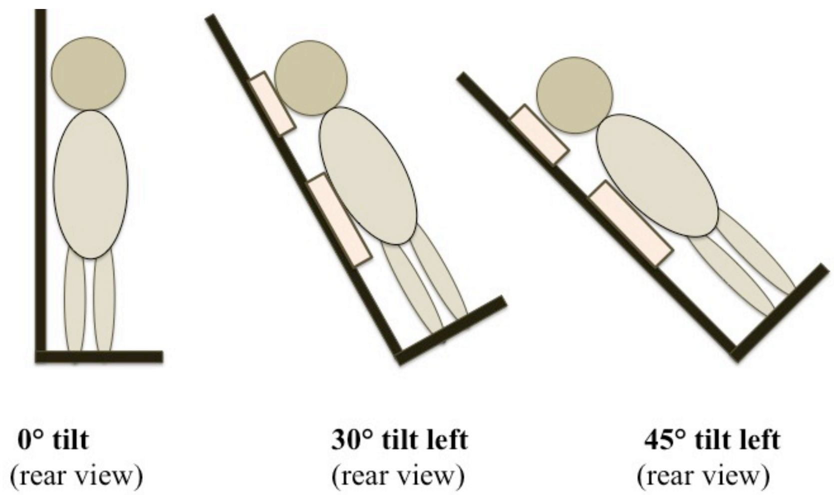


Figure 2.1. Body positions used in Experiment 1. The head was always aligned with the body.

Test rod

A hollow glass rod (30.5 cm long, 0.9 cm dia) was fitted with a blue cold-cathode light so that it could be illuminated from the interior. The rod was mounted on a motor (Applied Motion Products 23Q-3AE Integrated Stepper Motor), which was masked by a large circular sheet of black card to avoid it being illuminated by the light from the rod. The rod was viewed through a circular window that obstructed peripheral vision. The entire apparatus could be adjusted so that the center of the rod remained aligned with the nose of the participant. The apparatus was arranged to provide the participant free access to the rod with their right hand.

2.2.3 Procedure

Participants were assigned to one of three experimental conditions based on the tilt of the board: 0° (upright), 30° left or 45° left. Participants stood or lay against the tilted board with their left ear down. During the experiment the lights in the test room were turned off to remove external visual cues to orientation.

On each trial the motor drove the rod to a test orientation and a 400Hz beep indicated the trial had started. When the prompt beep sounded, participants were asked to judge whether the probe rod was tilted to the right or left of gravitational vertical (i.e., "Would the rod tip over to the left or to the right?"). They indicated their response on a mouse held in the left hand (left-click for "left" and right-click for "right"). Test orientations were selected by an adaptive staircase algorithm (QUEST, Watson & Pelli, 1983), which was optimized to estimate the point of subjective equality (PSE) of participants' underlying psychometric functions. This particular method was chosen because it is an efficient method of determining perceived vertical while remaining robust against manual adjustment errors. Following a response, the rod was moved by the motor to a new orientation determined by the QUEST algorithm and a 400 Hz beep prompted the participant to make the next judgment.

The motor moved at a constant velocity and pre-set acceleration and deceleration; a one second lag was introduced between the rod arriving at the final destination and the sound of the beep. Inter trial intervals ranged between roughly 2-3 seconds. The motor emitted minimal noise while changing position, which did not reflect the direction of movement. The rod remained static at the test orientation until a response was made.

The experiment was performed in a block design, with blocks occurring in random order. In the SVV block, the rod illuminated at the same time as the prompt beep, and participants made their left/right judgments by sight. After a mouse-button response was made, the light turned off and remained off until the next test orientation had been reached. In the SHV block, the rod remained dark throughout and participants were instructed to close their eyes. Upon being prompted by the beep, participants reached out with the right hand and felt the orientation of the rod. They then indicated their response on the mouse using the same hand, as a means of resetting arm position between trials. In the bimodal block, the rod was illuminated simultaneously with the prompt beep, and participants reached out to feel the tactile orientation of the rod as well. In this block participants were explicitly instructed to use both cues to estimate the rod's orientation (see Fig 2.2).

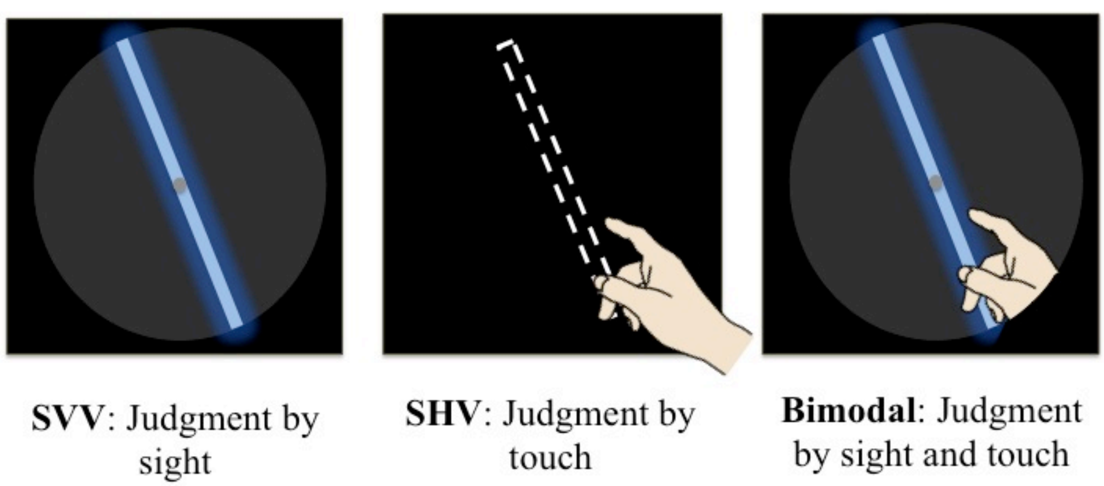


Figure 2.2. The three within-subject experimental stimuli in Experiment 1. Participants completed a block of 40 trials with each stimuli at a whole body tilt of either 0° (upright) 30° left or 45° left.

The QUEST was instructed to run for 40 trials in each block; results were checked following each block to confirm the staircase converged. In addition, there were 10 SVV training trials run at the beginning of the experiment to familiarize participants with the test paradigm and ensure they understood the experimenter's instructions. Thus, the experiment consisted of 130 trials total, with breaks between conditions. The experiment took roughly forty-five minutes to complete.

2.2.4 Convention

For all data reported, 0° is defined as true gravitational upright. Positive values indicate a clockwise tilt, and negative values indicate counterclockwise tilt from the point of view of the participant. In our convention therefore participants were aligned at 0°, -30°, or -45°, with the left ear down.

2.2.5 Data Analysis

The adaptive Bayesian algorithm used (QUEST; Watson & Pelli, 1983) was given initial estimates of a PSE of 0° (no bias) and a standard deviation of 20° (the QUEST creators suggest a liberal starting value to optimize convergence). Each participant yielded a PSE estimate for each of the three conditions. A plot of individual scores showed the PSEs of left-handers fell within the same range as those of right-handers, thus left-hander scores were included in the analysis (see also Tesio et al, 2011, who found no differences in SVV errors due to sex or handedness, and Tarnutzer et al., who found no differences in SHV error from sex or handedness).

PSEs were analyzed using a mixed-model 3x3 ANOVA (tilt x modality), with tilt a between-subjects variable and modality a within-subjects variable. Additionally, for each level of tilt, three t-tests were performed to identify if a significant bias in PSE from 0° was present in conditions; a step-up FDR adjustment was made to correct the significance threshold for these nine comparisons (Hochberg & Benjamini, 1990), with *q* set at 0.05.

2.3 Results

The PSE scores indicated the estimate of participants' perceived gravitational vertical in each condition. The mean PSEs for the tested conditions are shown in Table 2.1 with standard errors, and are plotted in Figure 2.3 with 95% confidence intervals.

Body tilt (degrees)	**PSEs (degrees)**		
	SHV	**SVV**	**Bimodal**
0	0.4 ± 0.7	-0.7 ± 0.3	-0.6 ± 0.3
-30	1.4 ± 1.0	0.02 ± 0.7	-1.3 ± 0.7
-45	2.4 ± 1.7	-4.0* ± 1.2	-3.6* ± 1.0

Table 2.1. Means and standard errors in degrees for each block (SVV, SHV and bimodal) by body tilt. The * indicates a mean significantly different than 0° (true gravitational vertical) at $p<0.05$.

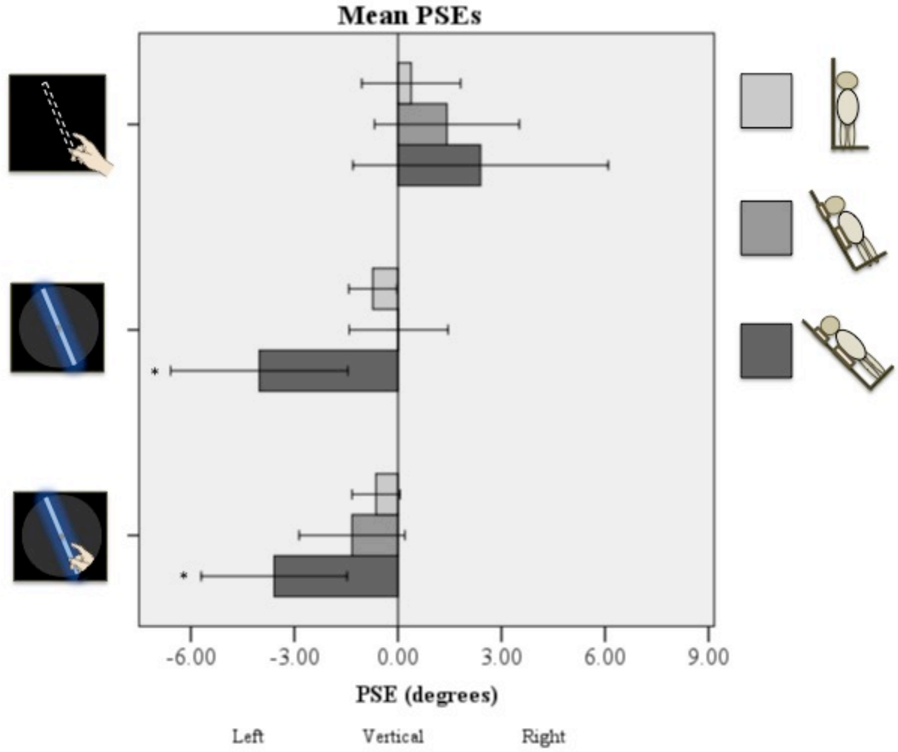


Figure 2.3. Means PSEs in degrees for each block (SVV, SHV and bimodal, shown on the left of histogram) by body tilt (shown on the right of histogram). Negative values indicate a leftward tilt and positive values indicate rightward tilt. The * indicates a mean significantly different than 0° (true gravitational vertical) at p<0.05. Error bars are 95% confidence intervals.

A mixed-model ANOVA of PSEs found a tilt x modality interaction was significant, $F(4,90)=4.05$, $p=0.005$. There was also a main effect of probe modality, $F(2,90)=14.66$, $p<0.001$. Thus, the type of measure used (SVV, SHV or bimodal) differentially shifted perception depending on the amount of whole-body tilt. Figure 2.3 shows that mean responses for SVV and bimodal tilted further towards the body (A effect), while SHV tilted away from the body (E effect) as tilt increased.

Nine t-tests were performed to compare each mean PSE against the unbiased vertical (i.e., 0°). P-values were corrected using a stepwise FDR procedure with a q of 0.05. Of the nine conditions, only the SVV and bimodal PSEs at a -45° were significantly different from 0°, $t\,(15)=-3.34$, $p=0.005$ (SVV) and $t\,(15)=-3.59$, $p=0.003$ (bimodal). The bias in both of these means indicated an A effect, or a tilt in the direction of body tilt.

2.4 Discussion

Experiment 1 sought to directly compare the SVV and SHV in the same subjects using a robust forced-response (FR) paradigm. In addition, I also tested a bimodal probe of verticality perception as an exploration of the integration of visual and haptic cues to alignment with gravity vertical, and potential suppression of unimodal modality-specific errors.

2.4.1 Diverging SVV and SHV

SVV results showed an A effect as tilt increased. That is, as participants were tilted away from upright, their visual estimates of gravity skewed further in the same direction as tilt, although this bias only became significant at 45° of tilt. These findings are consistent with the previous reports of an A effect in the SVV using the ADJ method (e.g., Ceyte et al., 2009; Barra et al., 2010; Wade & Curthoys, 1997; Van Beuzekom & Van Gisbergen, 2000; De Vrijer et al., 2004; Tarnutzer at al., 2009b), validating both our procedure and the findings of Baccini et al. (2014) who found ADJ and FR methodologies produced similar results. In contrast, SHV errors trended towards an E effect (bias opposite body tilt) as tilt increased, but did not reach significance. This is also consistent with previous findings of minor or no biases in SHV using the ADJ method (e.g., Schuler et al., 2010). The bimodal probe appeared to follow the pattern of SVV (trended towards an A effect, significant at only 45°). The visual component of the bimodal probe dominated this task; this result will be revisited and expanded upon in Chapter 4.

Importantly, the results of the ANOVA showed a significant modality x tilt interaction, suggesting that SVV and bimodal probe generated distinct results from SHV. Specifically, across levels of tilt, SVV and bimodal responses had a trajectory opposite that of SHV. As Figure 2.3 illustrates, the difference appears to be driven by the SVV and bimodal probe trending towards the body midline, while the SHV trended away from it.

These results indicate that SVV and SHV estimates for the same individuals are opposite in nature. What might be the underlying cause of this divergence, given that both estimates are intended to probe the same percept (an object's alignment with perceived gravity vertical)? One possibility for the different biases in visual- and haptic- based versions of this task is that object orientation is misperceived in different ways depending on the modality used (e.g., ocular torsion influencing vision, use of a specific hand in haptic) (Schuler et al., 2010). Thus, the bias may influence the perceived object orientation while the underlying percept of gravity may be intact. Another possibility is that the estimates of gravity vertical invoked while doing the SVV and SHV tasks are somehow different in nature, either in their differential use of a prior (MacNeilage et al.,

2007) or differential weighting of egocentric components (Clemens et al., 2011). This latter possibility will be explored in the following two experiments.

CHAPTER 3: Contributions of the head and body to SVV and SHV: A role for the vestibular system in tactile perception of orientation?

3.1 Introduction

In Chapter 2, I demonstrated that visual measures of object verticality and haptic measures produce opposite biases as a person is tilted laterally away from gravitational upright; the SVV tilts towards the longitudinal body axis, and the SHV trends away from it. The following experiment investigates the possibility that the estimate of gravity vertical invoked by SVV and SHV tasks differs in some manner, whether by the weighting of respective egocentric components in determining gravity vertical (e.g., a heavier weighting of trunk vs. head), or by the presence of some prior which influences one estimate, but not the other. In order to test the respective contributions of head- and body- based indicators of gravitational upright, I varied the tilt of the body and head with respect to gravity separately in the same subjects, and measured their SVV and SHV. I hypothesize that, consistent with previous work (discussed in section1.2), head-only tilt will evoke SVV errors, and body tilt will evoke smaller SVV errors. In contrast, I hypothesize that body tilt will have a more pronounced effect on SHV than head tilt as previous research has shown head-only tilt does not evoke SHV errors (Tarnutzer et al., 2012a).

To further isolate the possible prior, we used galvanic vestibular stimulation (GVS) to add noise to the vestibular system. GVS introduces an artificial vestibular signal by applying a mild electrical current to the mastoid process behind either ear via small electrode. The specific simultaneous difference in voltage between the two electrodes determines the perceived vestibular input, and can invoke compensatory postural and walking behaviours (Fitzpatrick et al., 1999; Fitzpatrick et al., 1994). Here I used an alternating sum-of-sines voltage pattern, with dominant frequencies at 0.16, 0.33, 0.43 and 0.61 Hz. The stimulation was bilateral and bipolar (one ear received positive current while the other received negative current, and vice versa). This pattern, explained in more detail in MacDougall et al., (2006) has been shown to generate a subjective sensation of swaying left and right while in fact stationary. Due to the unpredictable nature of the sum-of-sines signal (i.e., the stimulation for every trial is unique) it is difficult to adapt to the swaying sensation, and thus this method effectively creates prolonged vestibular noise (Moore et al., 2006; MacDougall et al., 2006).

It has been theorized that priors are weighted relatively more heavily when sensory noise is greater (i.e., when the sensory information is less reliable) (e.g., MacNeilage et al., 2007). If the "idiotropic" prior (discussed in section 1.2) is preferentially accessed by SVV, as argued by Schuler et al., (2010), GVS should induce stronger SVV A effects, while not affecting SHV.

3.2 Methods

3.2.1 Participants

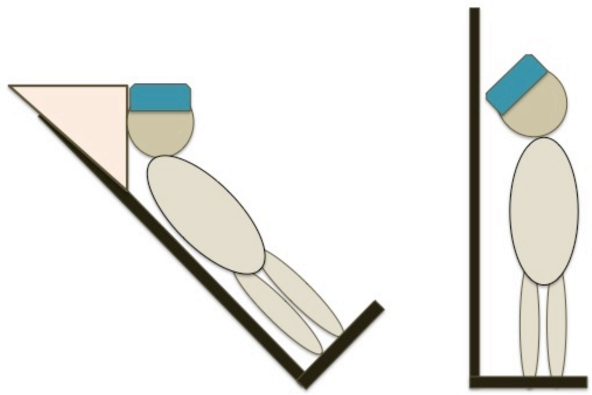
Thirty-two participants (aged 18-36, 14 female and 18 male) took part in this experiment. Participants were undergraduate and graduate students of York University and members of the North York community (the latter were recruited by word of mouth). Participating undergraduate students received a 1% bonus credit towards their

Introduction to Psychology course in exchange for participating; non-undergraduate participants did not receive any compensation. All participants had normal or corrected-to-normal visual acuity. Two of the participants identified themselves as left-handed, and one identified as ambidextrous. All experiments were approved by the ethics board of York University and were run according to the principles of the Declaration of Helsinki.

3.2.2 Apparatus

Platform

Two body positions were used in this experiment, with the body tilted and head upright ("body-tilt") or body upright and head tilted ("head-tilt"; see Fig 3.1). In the body-tilt position, participants lay on their left side on a wooden board tilted 45° with foot support and a stiff triangular pillow propping the head so that it was aligned with gravity. In the head-tilt position, participants were asked to stand against a vertical board with their head tilted to the left side by 45° (see Fig 3.1). Head angles were measured with a head mounted apparatus consisting of a protractor and spirit level, which were compared against a plumb line. Participants were situated with the nose approximately 40 cm from the rotational center of a test rod.



Body-tilt position: Body tilted 45° left, head upright (rear view)

Head-tilt position: Body upright, head tilted 45° left (rear view)

Figure 3.1. Rear view of the body positions used in Experiment 2

Test rod

This experiment used the same test stimulus as experiment 1; see section 2.2.2 for details.

Galvanic vestibular stimulation

Vestibular noise was generated by a GVS system (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada), a head-mounted system connected via simulated serial port (USB) to a computer, through which it was controlled by a MATLAB program. Two electrodes (1.25” dia, 9000 series, Empi Recovery Sciences, St. Paul, Minnesota, USA) were placed on the mastoid process behind either ear and secured with tape. The GVS was armed to send an alternating sum-of-sines voltage (see above) between electrodes (maximum current of 5ma, sampling rate of 25ms). Stimulation was bipolar such that one electrode emitted the inverse voltage of the other electrode. The specific parameters and pattern of stimulation were taken from Moore et al., (2006) and MacDougall et al., (2006) and have been shown to induce a subjective sensation of swaying left and right while the head is in fact stationary. Some participants reported seeing a transient illusory sway of the test stimulus during GVS, while others reported a mild sensation of whole-body sway. Researchers were present during testing to ensure participants held still in the required pose throughout the experiment.

Prior to testing in the GVS condition, the GVS was turned on briefly (for approximately 10s) to familiarize participants with the sensation and ensure the electrodes were well attached. During this initial phase one female participant became very disoriented and could not stand unsupported. This individual was removed from the experiment immediately and did not complete any testing.

3.2.3 Procedure

The experiment was a mixed design. Participants were assigned to either a GVS or control condition (between-subjects variable), and completed both SVV and SHV in both positions (within-subjects variables). On each trial the motor drove the rod to a test orientation. In the GVS condition, the current began immediately when the test orientation had been reached. After a 1.5 s lag a 400Hz beep indicated the trial had started. Participants were instructed to judge whether the probe rod was tilted to the right or left of gravitational vertical ("would the rod tip over to the left or to the right?"). They indicated their response on a mouse held in the left hand (left-click for “left” and right-click for “right”). The rod remained static at the test orientation until a response was made. In the GVS condition, the current was stopped when a response was made. The rod then moved to a new orientation and the next trial began. Test orientations were selected by an adaptive staircase algorithm (QUEST, Watson & Pelli, 1983).

The SVV task procedure was the same as experiment 1 (described in section 2.2.3), with the exception that, in this experiment, the test rod was illuminated 1s *after* the prompt beep to allow more time for the GVS to take effect. The SHV procedure was the same as in experiment 1.

All participants completed four different testing blocks: SVV and SHV in the body-tilt position and the same two tasks in the head-tilt position. The four blocks were run with or without GVS stimulation, depending on participants’ assigned test condition. Test blocks were randomly ordered, but due to the difficulties of moving the stimulus between the tilted and upright platforms, all body-tilt position tasks were completed together in sequence and the same for head-tilt position. All experimental blocks were completed in a dark room.

For each block, the QUEST was configured to run for 40 trials, which took approximately 7-10 minutes to complete. After each block the experimenter checked the staircase to confirm it had converged. Thus, the experiment consisted of 160 trials total, with breaks between conditions. Including instruction and equipment set up the experiment took approximately 45 minutes.

3.2.4 Convention

The same convention as Experiment 1 was used here; see section 2.2.4 for details.

3.2.5 Data Analysis

The adaptive Bayesian algorithm used (QUEST; Watson & Pelli, 1983) was given initial estimates of a PSE of 0° (no bias) with standard deviation of 20° (Watson & Pelli suggest a liberal starting value to optimize convergence). Each participant yielded a PSE estimate for each of the four conditions. A plot of individual scores showed left-hander PSEs all fell within the range of right-hander PSEs, and thus left-handers were included in the analysis.

PSEs were analyzed using a mixed-model 2x2x2 ANOVA (GVS x Position x Modality), where GVS was a between-subject variable and all others were within-subject variables. Additionally, 8 t-tests were performed to identify if a significant bias in PSE from 0° was present in each condition; a Benjamini-Hochberg step-up FDR adjustment was made to correct for these 8 comparisons (Hochberg & Benjamini, 1990).

3.3 Results

PSE scores indicated the perceived direction of gravity in each experimental condition. Mean PSEs and standard errors for each test condition are shown in Table 3.1, and are plotted in Figure 3.2 with 95% confidence intervals.

Position	PSEs (degrees)	
	SVV	SHV
Body tilt (control)	-1.6* ± 0.4	-3.1* ± 1.1
Head tilt (control)	-2.4* ± 0.9	0.6 ± 1.2
Body tilt (GVS)	-0.7 ± 0.4	0.2 ± 1.5
Head tilt (GVS)	-1.1 ± 1.2	9.3* ± 1.8

Table 3.1. Means and standard errors in degrees for SVV and SHV by condition. The * indicates a mean PSE significantly different than 0° (true gravitational vertical) at $p<0.05$.

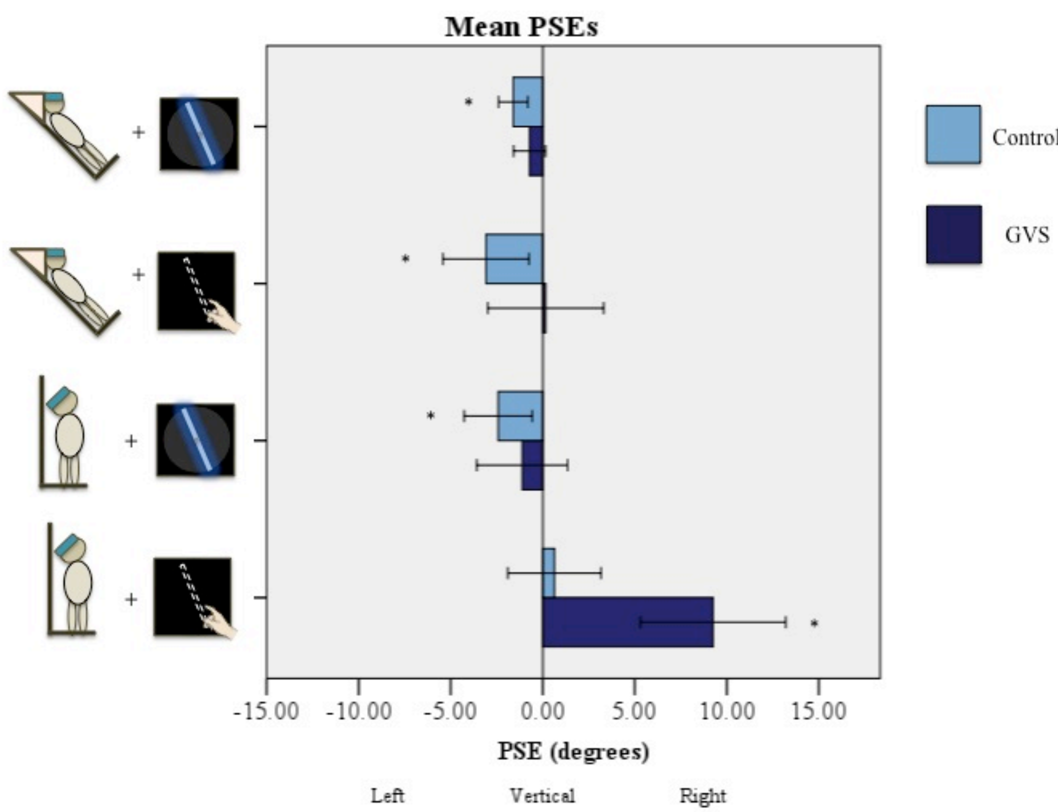


Figure 3.2. Mean PSEs (in degrees) for SVV and SHV by position. Negative values indicate a leftward tilt and positive values indicate rightward tilt. Head and body tilts and the tests applied are indicated by the cartoons on the left side. Pale blue bars are without GVS, dark blue bars are with GVS. The * denotes a score significantly different than 0° (true gravitational vertical) at $p<0.05$. Error bars are 95% confidence intervals.

A mixed-model ANOVA of PSE scores found a significant interaction of modality x position, $F(1,29)=24.03$, $p<0.001$, indicating that the individual tilt of head or body had a different effect on perceived vertical depending on modality used. Additionally, there was a significant interaction between GVS x position, $F(1,29)=9.46$, $p=0.005$, suggesting that the tilt of the head vs. body modifies the effects of GVS on perception. There was also a main effect of modality (SVV or SHV), $F(1,29)=15.64$, $p<0.001$, position (body-tilt or head-tilt), $F(1,29)=16.57$, $p<0.001$ and GVS (on or off), $F(1,29)=13.58$, $p=0.001$.

Eight t-tests were used to compare PSE scores in each condition to true gravitational vertical (i.e., 0°). P-values were measured against a significance threshold controlling for the False Discovery Rate with a q of 0.05. Control SVV and SHV scores in the body-tilt position both showed a significant A effect, t (15)=-4.31, $p=0.001$ (SVV) and t (15)=-2.81, $p=0.013$ (SHV). In the head-tilt position without GVS, only SVV showed a significant A effect, t (15)=-2.79, $p=0.014$. SHV did not significantly differ from true vertical in this condition. While head and body tilt both produced an A effect in SVV, only body tilt produced a bias in SHV. Curiously, this bias was in the direction opposite to the (non-significant) trend in SHV in Experiment 1 (c.f., Fig 2.3) during whole-body tilt.

Of the GVS conditions, the only significantly biased PSE was the SHV with the head tilted to the left (position B), t (14)=5.04, $p<0.001$. The source of this pronounced E effect, and the surprising absence of a visual A-effect, will be discussed below.

3.4. Discussion

This experiment had two goals: 1) to identify the relative contributions of head and body position to SVV and SHV and 2) to identify the relative contributions of an idiotropic prior to SVV and SHV by adding artificial vestibular noise and thus promoting the influence of such a prior.

3.4.1 Relative contribution of head and body positions

To address 1): an A effect was found for SVV during both head-only and body-only lateral tilt with no GVS. That is, in all SVV non-GVS conditions there was significant shift of the verticality estimates in the same direction as the tilted body part. This is supported by previous work that shows head tilt drives SVV errors, while the trunk plays a secondary role (Guerraz et al., 1998; Tarnutzer et al., 2010). In contrast, a bias in SHV only occurred in the body-tilt only condition, replicating Tarnutzer et al.'s (2012a) finding that head-tilt only postures did not significantly bias the SHV. Curiously, in the body-tilt only condition, the bias was also in the direction of tilt (A effect) as opposed to the opposite trend in responses elicited by the whole-body roll used in Experiment 1.

Results of the ANOVA confirmed a difference in performance in the same subjects on SVV and SHV tasks. The significant interaction between position x modality suggests that the egocentric components of the head and body play a different role in the two tasks. However, the reversal in the SHV bias compared to Experiment 1 suggests that it is not merely a differential weighting of body parts in SVV and SHV, but also their relative configuration that influences SHV.

In sum, the position of different body components relative to gravity (head or trunk) plays different roles in SVV and SHV tasks, with the head and the body influencing SVV and only the body influencing SHV in a complex fashion. This is further evidence for an underlying difference in the nature of the two tasks.

3.4.2 Role of the idiotropic prior

To address 2), we introduced artificial noise to the vestibular system using GVS. When two cues are combined to form an internal estimate, the cues are weighted according to how reliable they are (e.g. Ernst & Banks, 2002). As sensory noise increases, the idiotropic prior should become weighted relatively more heavily, resulting in a more pronounced bias towards the body's longitudinal axis (see Chapter 4 for more on cue integration). If we attribute the divergence in SVV and SHV under whole-body roll to a prior affecting one estimate but not the other, GVS should increase the A effect in SVV but not in SHV. Yet the GVS x modality interaction was not significant, and from the data in Figure 3.2 it becomes clear why. The addition of GVS actually *negated* the previously found SVV biases, resulting in SVVs that were no different from accurate. This is the opposite of what I hypothesized based on an increased weighting of an idiotropic prior, and calls into question the nature of this prior and whether it is in fact tied to the visual/vestibular system at all.

Anecdotally, some participants mentioned they thought the visual stimulus was "rocking" or "swaying" while the GVS was on, suggesting that the stimulation may have triggered the counteroll reflex (GVS has been shown to trigger OCR and cause reflexive eye movements; Kleine et al., 1999; Severac Cauquil et al., 2003). It's possible that with this additional motion of the eyes, the *average* position of the retina could be better ascertained (compared to static tort), and thus errors in object perception from uncompensated-for ocular torsion might be mitigated, resulting in an SVV free from response bias. The interaction between SVV, GVS and torsion-based eye movement merits further investigation, and will be the focus of future research.

In addition to suppressing a visual A effect in the SVV, GVS also suppressed the A effect found in the SHV-with-body-tilt condition. Remarkably, the SHV-with-head-tilt condition under GVS produced a notably large E effect. To my knowledge, this is the first finding of this kind, and implicates the vestibular system in SHV, despite the fact that under normal conditions head tilt does not produce an SHV bias. These results, along with the reversal of the bias elicited by body-only tilt (this experiment) vs. whole body tilt (experiment 1), point to a complex interaction between the position of the body, vestibular input and the arrangement of the neck as the source of SHV errors.

Another possible explanation for the pattern of responses in SVV and SHV under GVS is that the stimulation introduced an overall shift of verticality percepts to the *right* (away from head or body tilt). This could counteract underlying A effects in the three conditions in which they were previously reported (SVV in both positions and SHV + body tilt), and might generate an E effect in the condition where responses were previously accurate (SHV + head tilt). It is possible this overall rightward shift of perceived verticality is due to the brain's interpretation of the ambiguous GVS signal as a rightward shift of the head, the body, or both, while tilted left. Preliminary work by Harris and Makooie (in progress) suggests that sinusoidal GVS may be interpreted as different kinds of motion depending on the body position adopted during stimulation. Though we use a different signal, intended to simulate pure vestibular noise (sum-of-sines), it is possible that this signal is still interpreted by the brain as directional motion or static tilt. This could conceivably explain the absence of an exaggerated prior with increased vestibular noise, although it still implies a role for the vestibular system in SHV. Future work quantifying the subjective perceptions associated with different GVS signals is needed in order to assess the likelihood of this alternative explanation.

3.4.3 Summary

Experiment 2 showed a differential weighting of the head and trunk in SVV and SHV, and a role for the relative configuration of the head and body in the directionality of SHV errors. I saw little evidence for the existence of a systematic prior for either task during increased vestibular noise. The additional vestibular noise skewed the SHV opposite the direction of tilt when the head was tilted, but otherwise appeared to suppress or counter verticality biases.

The question put forth at the beginning of this experiment was whether the estimate of gravity vertical invoked by SVV and SHV tasks differs in some manner. While this study does not support differential access to a prior, it does suggest that a differential weighting of body components may exist. Experiment 3 explores the question of whether this relative weighting constitutes two distinct gravity estimates, or a single underlying estimate that is accessed differentially by vision and touch.

CHAPTER 4: Degraded neck proprioception promotes optimal integration of subjective visual and haptic verticals

4.1 Introduction

In Chapter 2, I demonstrated that SVV and SHV measures produced diverging estimates of verticality, with SVV showing a bias towards the body (A effect), and SHV trending away from the body (E effect), as body tilt increased in the roll plane. In Chapter 3, I showed that incongruent roll tilts of the head and body had a differential effect on SVV and SHV, implicating a stronger influence of head position on SVV errors, and an influence of body position on errors in both measures. Chapter 3 also demonstrated that GVS-induced vestibular noise suppressed SVV errors, contrary to what we would predict if a prior had caused them (see section 1.2). Vestibular noise also suppressed SHV errors during body-only tilt, but generated a large E effect in the head-only tilt condition. These results, taken together, suggest that SVV and SHV tasks differ not only in the modality they use as a probe, but in the nature of the verticality estimate they access. The following experiment contrasts two different models of gravity estimation in the hopes of elucidating this difference.

4.1.1 Two models of subjective verticality

Schuler and colleagues (2010) compared SVV and SHV using the adjustment method and found that the trial-to-trial variability of estimates for both measures was correlated across different magnitudes of roll tilt (corresponding, they argue, to the suboptimal performance of the otoliths with increased tilt). The authors suggest that SVV and SHV must access the same underlying estimate of the gravity vector, with modality-specific influences producing their respective biases.

In contrast, Clemens and colleagues (2011) model gravity perception as having two distinct egocentric reference frames; one infers the position of the gravity vector using sensory information about the head's position in space, while the other infers the direction of gravity from sensory information about the body in space. Proprioceptive knowledge of neck position allows sensory information about body position to inform the head position estimate, and vice versa (what Clemens and colleagues refer to as an "indirect pathway"). For example, if the head is perceived as being rolled to angle h, according to head-based sensory input, the body is perceived as rolled by angle b according to body-based sensory input, and proprioceptive information about neck angle indicates the head is tilted on the body by z degrees, the final perceived head position will be a weighted averaging of h and b-z (which can then be used to infer the gravity vector). The weighting of these individual components, according to maximum likelihood estimation theory (see below), would then be based on the reliability of the respective sensory signals used to detect them. A simplified diagram of the Clemens model is shown in Figure 4.1.

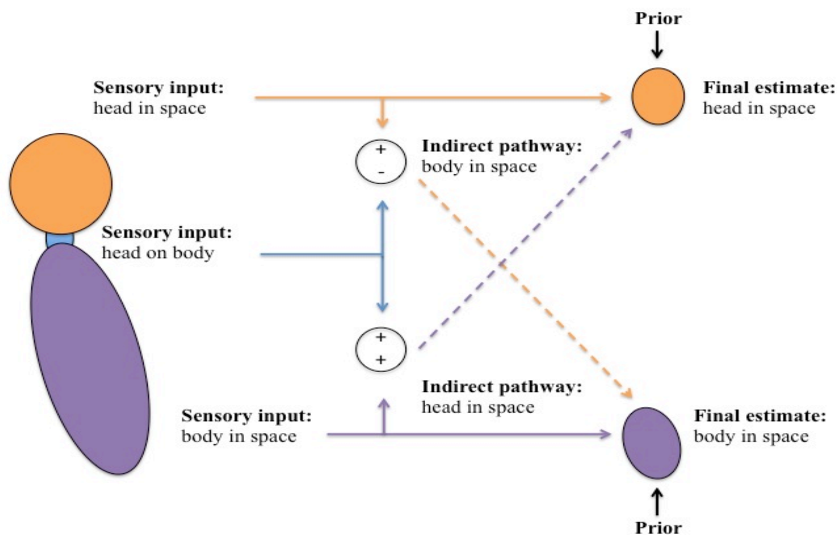


Figure 4.1. A simplified version of the two-estimate model proposed by Clemens et al. (2011). Final estimates of head position are informed by direct sensory input from head-based sensors, as well as indirect input from body-based sensors (modified by perceived orientation of the head on the body). Final estimates of body position are informed by direct input from body-based sensors, and indirect input from head-based sensors (again, modified by perceived head-on-body angle). Note that in their model, Clemens and colleagues include two idiotropic priors that modify the final head and body position estimates. Each contributing input to the final estimates is weighted according to the relative reliability of the signal, and the weighted values are averaged to determine the final estimate. This estimate can then be used to infer the direction of gravity.

According to Clemens et al. (2011) the two egocentric references (head and body) are accessed preferentially according to the task at hand. The authors show evidence that SVV relies on the head-in-space estimate to infer the position of gravity vertical, but do not address the SHV. I argue that the SHV is most likely to access the body-in-space estimate, as the results of Experiment 2 show that body position plays a stronger role in this measure.

In order to compare the models of Schuler et al. (2010) and Clemens et al. (2011), this experiment revisits the bimodal measure of verticality introduced in Chapter 2, and adopts a testing procedure to measure not only the PSEs of all three verticality estimates (SVV, SHV and bimodal), but their precision as well, to determine whether the combination of subjective visual and haptic verticality percepts is indicative of a single gravity estimate or multiple estimates. The rationale for this will be discussed in the following section.

4.1.2 Principles of optimal sensory integration

When multiple cues to a single event are available, an optimum strategy for using all the information is to average the cues weighted according to each cue's reliability. This has the effect of producing the most reliable (lowest variance) estimate mathematically possible and is known as Maximum Likelihood Estimation (MLE, Ernst & Banks, 2002). There are many examples of MLE integration of sensory inputs (e.g., Ernst & Bülthoff, 2004; Vroomen et al., 2004; Byrne & Crawford, 2010), including for assessing vertical by combining somatosensory and vestibular cues (Clemens et al., 2011) and visual cues and vestibular information (MacNeilage et al., 2007). The MLE model predicts the weighting of two sensory inputs (e.g., tactile cue *H* and visual cue *V*) according to the inverse of their normalized variance (Equation 4.1):

$$W_V = \frac{1/\sigma^2_V}{1/\sigma^2_H + 1/\sigma^2_V} \qquad W_H = \frac{1/\sigma^2_H}{1/\sigma^2_V + 1/\sigma^2_H} \tag{4.1}$$

where σ^2_V is the variance (standard deviation squared) of responses to cue *V*, and σ^2_H is the variance in the responses to cue *H*. The predicted response to both cues presented simultaneously (S_{VH} can then be calculated using a weighted average (Equation 4.2) of each component's response (S_H, S_V).

$$S_{VH} = W_V S_V + W_H S_H \tag{4.2}$$

The Maximum Likelihood Optimization model also quantitatively predicts that the standard deviation of the combined judgments should be lower than either of the single-cue judgments of each participant according to equation 4.3:

$$\sigma_{HV} = \sqrt{\frac{\sigma^2_H \sigma^2_V}{(\sigma^2_V + \sigma^2_H)}} \tag{4.3}$$

Where σ^2_H is the variance for cue *H,* σ^2_V is the variance for cue *V*, and σ_{HV} is the predicted standard deviation (SD) of the combined condition.

An important principle of MLE is that in order for two cues to optimally combine according to equations 4.2 and 4.3, they must have *independent sources of noise.* Ernst (2012) notes, "If the noise distributions of the estimates are positively correlated there is still a benefit from integration in the form of an increased reliability. However, this benefit will be less compared to the uncorrelated case and it is less the higher the correlation" (Ernst, 2012, p.535). If SVV and SHV indeed access separate estimates of gravity vertical (Clemens et al., 2011), then sensory integration of the two signals (haptic and visual) in a bimodal task could be optimal. If they share an underlying estimate of the direction of gravity (Schuler et al., 2010), then we would expect a high positive correlation in sensory noise, and the subsequent precision will be significantly worse than that predicted by equation 4.3.

4.1.3 Testing PSEs and within-subject SDs

In order to test these assertions, I needed to use a methodology that was optimized to measure not only PSEs but also the standard deviations of participants' judgments. Experiments 1 and 2 used an FR method with 40 trials, with test angles chosen by a QUEST adaptive staircase (Watson & Pelli, 1983) optimized to find the PSE. Because this test staircase hones in on the PSE, its test points are distributed over a very small range of angles and fitting a slope to this data is unreliable. For Experiment 3, I opted to use another adaptive staircase, the psi-method (Kontsevich & Tyler, 1999) which tests the shoulders of the psychometric function rather than the PSE directly, and thus can estimate both PSE and the standard deviation (SD) of a participant's psychometric function, albeit with a great deal more required trials. The results of SHV and SVV using QUEST and psi will be compared in section 4.4.

4.1.4 Predicting optimal bimodal scores

To predict optimal bimodal verticality estimates, it's necessary to test unimodal verticality estimates (i.e., SVV and SHV) to determine the PSEs and SDs associated with these measures for each individual participant. These unimodal scores can then be used to calculate the optimal bimodal PSE and SD for each individual. I can then compare raw bimodal scores with the MLE-predicted scores to determine whether or not they differ (the correct testing procedure for this is an equivalence test, but since it involves setting arbitrary limits as to what it deemed 'equivalent' in this case, I will use standard paired Student's t-tests. Cribbie and colleagues, 2004, have shown that for small sample sizes, a t-test is just as or more effective at detecting statistical equivalence compared to equivalence tests).

Data from Chapter 2 suggested that it is the visual component that dominates the bimodal probe of perceived verticality. Pilot tests using the psi method confirmed this, and so I developed a second visual stimulus, where the presented line was shorter and obscured by a diffusing screen, and tested a second SVV and bimodal measure using this stimulus. I refer to this version of the visual stimulus as the "blurry visual stimulus" (see Figure 4.4). The aim was to make the visual task more difficult and thus increase the variability of responses associated with the visual stimulus in order to make the reliability of the visual and haptic cues more comparable. MLE then predicts the two cues would be more evenly weighted (thus avoiding total visual dominance, or capture).

4.1.5 Degrading the indirect pathway

Though I aimed to contrast the models of Schuler et al. and Clemens et al. by identifying whether there was shared noise in SVV and SHV (pointing to Schuler et al.'s shared underlying estimate of gravity), there is in fact shared noise in the two-estimate model as well, in that the indirect pathway can be used to share head-based and body-based sensory information concerning the relative positions of the head and body between the two final egocentric references for gravity. Since these “indirect pathways” are mediated by neck proprioception (i.e., the head-on-body estimate, see Figure 4.1), degrading this proprioceptive information should lead to a degraded indirect pathway, thus effectively ‘decoupling’ head- and body-based estimates of gravity vertical. To do this, I added an experimental condition where the SHV, the SVV with the blurry stimulus and the bimodal combination of the two measures were tested while mild vibration was applied to the dorsal muscles of the upper neck. This group of muscles has been implicated in head roll (Mayoux-Benhamou et al., 1997), and vibration of one side of this area was found to affect SVV as though the head were rolled toward the opposing side, while vibration of other nearby areas did not (McKenna et al., 2004). I posited that vibration of both sets of these muscles would introduce noise into the afferent signal associated with perception of head-on-body roll, and that any tendency to evoke an actual head movement percept would be cancelled out because of the bilateral application. This is, as far as I am aware, a novel application of neck muscle vibration. During the experiment, participants reported that the vibration was somewhat uncomfortable but not intolerable. The added noise was designed to effectively degrade the indirect pathway between head- and body-based gravity perceptions. If the bimodal condition were to show suboptimal integration in the control, no-vibration conditions but optimal integration in the neck vibration condition, this would be compatible with the idea that Clemens' indirect pathway was the shared source of noise in the control data, thus providing evidence for a two-estimate model of gravity perception. If suboptimal integration persists in the presence of vibration, it would suggest that the common source of noise preventing integration might be due to a shared underlying estimate of gravitational vertical.

4.2 Methods

4.2.1 Participants

Twenty participants (aged 21-60, 11 female and 9 male) took part in this experiment. Participants were undergraduate and graduate students and faculty of York University. All participants had normal or corrected-to-normal visual acuity. One participant identified as left-handed, and one identified as ambidextrous. All experimental procedures were approved by the ethics board of York University and were run according to the principles of the Declaration of Helsinki.

The two conditions of this experiment were completed with at least one month in between testing session 1 (control) and testing session 2 (vibration). The participants who completed both conditions are shown below in Table 4.1.

Control	Vibration
1	1
2	-
3	3
4	4
5	5
6	6
7	7
8	8
9	-
10	10
11	11
12	12
13	13
14	14
15	-
16	-
	17
	18
	19
	20

Table 4.1. Participants who completed both experimental conditions (separated by > 1 month between sessions)

4.2.2. Apparatus

Platform

Participants used the same platform described in Experiment 1, tilted 45° left (see section 2.2.2 and rightmost image in Figure 2.1).

Test rod

The test stimulus was the same as in experiments 1 and 2 (see section 2.2.2 for full description). In two of the test blocks the rod was clearly visible ("sharp visual stimulus"); in two additional blocks a plexiglass screen covered in a layer of vehicle window tinting with 5% visible light transmission (Gila Basic Super Limo Black 5%

Window Tint, http://www.gilafilms.com/en/Basic-Window-Tints.aspx) was set 30 cm in front of the rod. The rod was also masked with opaque tape such that only the middle 5cm was visible. This degraded visual stimulus will be referred to as the "blurred" visual stimulus below (see figure 4.4). In all conditions the apparatus was arranged, as in the previous experiments, so that participants were able to reach out and freely explore the rod by touch.

Neck Vibration

Vibration was applied to both sides of the upper dorsal neck via a pair of commercial handheld battery-operated vibrators (http://www.trojanvibrations.com/product/-vibrators-pulse-vibrator.do), which were embedded in foam blocks and held in place with a tensor bandage tied securely around the participant's neck (see Figure 4.2). The vibrators both had a circular surface of contact approximately 1 inch in diameter and a vibration frequency of 30 Hz (measured using a strobe light). They were placed on the upper dorsal neck muscles, approximately 1 inch below the base of the skull and one inch out to either side from the spine. In order to ensure consistent vibration intensity over time, the batteries were changed after every 2nd participant. The vibrators were used at their lowest continuous vibration setting, and were left on for the duration of each experimental block. The vibrators were turned off between experimental blocks.

Figure 4.2. Attachment of vibrating apparatus to the back of the neck. Vibrators were held in place using foam blocks and a tensor bandage tied around the neck.

4.2.3. Procedure

In the control testing session, participants completed five testing blocks: (1) judging orientation by touch with the eyes closed (SHV), (2) judging by sight with the sharply visible stimulus (SVV sharp), (3) judging by sight with the blurred stimulus (SVV blurred), (4) judging bimodally with touch and the sharply visible stimulus, (bimodal sharp), and (5) judging bimodally with touch and the blurred stimulus (bimodal blurred) (see Fig 4.3). In the vibration testing session, which took place at least one month later, the SHV, SVV blurred and bimodal blurred test blocks were repeated. Blocks were completed in a random order for each participant. All blocks were completed in a dark room. Procedures for SVV and SHV are the same as in experiment 1; see section 2.2.3 for details.

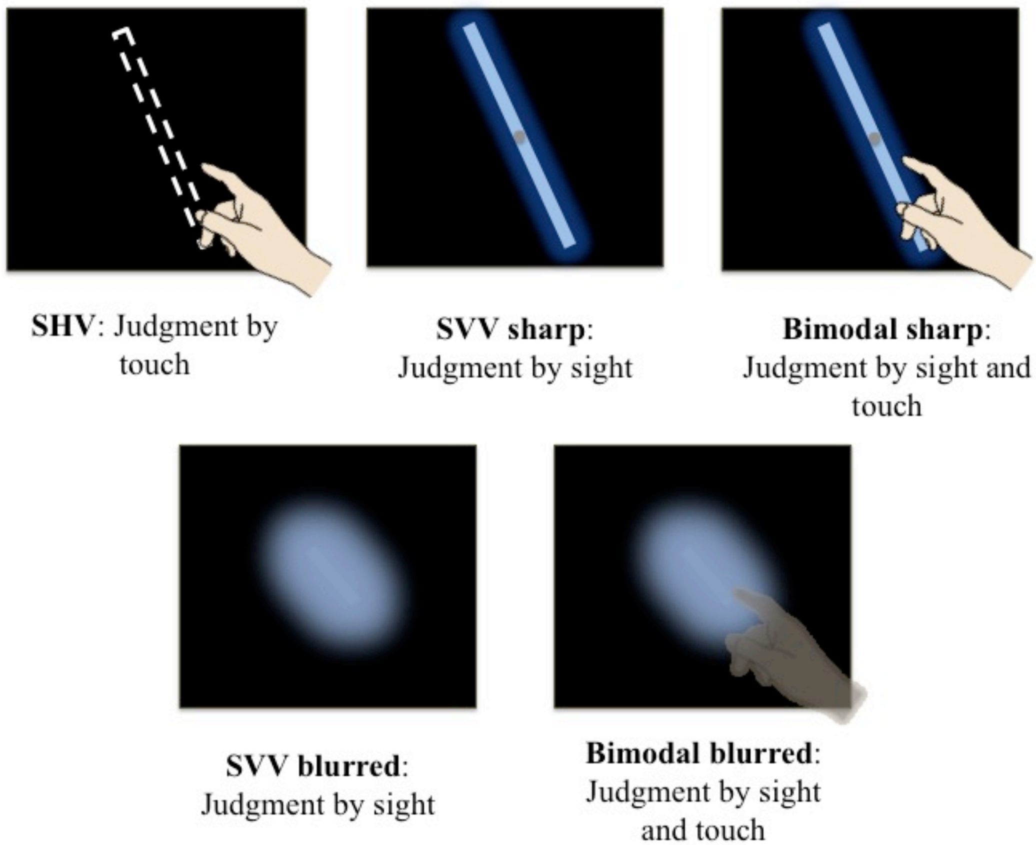


Figure 4.3. The five experimental stimuli used in the control (no vibration condition). In the vibration condition, only the SHV, SVV blurred, and bimodal blurred were tested.

Test rod orientations were selected by a Bayesian adaptive staircase (the psi-method, adapted for MATLAB from Kontsevich & Tyler, 1999), which estimated the point of subjective equality (PSE) and the standard deviation (inverse slope; SD) of participants' underlying psychometric functions. This particular method was chosen because it is optimized to accurately estimate within-subject standard deviations, i.e. within-subject precision.

For each of the five testing blocks, the psi algorithm was instructed to run for 150 trials, which took approximately 20 minutes to complete. After each block the experimenter checked results to ensure the staircase had converged. Thus there were 750 trials total in the control testing condition and 450 in the vibration condition. Participants completed all blocks in a testing session over a period of several days.

4.2.4 Convention

The convention here is the same for experiments 1 and 2; refer to section 2.2.4 for details.

4.2.5 Data Analysis

The testing algorithm used (psi-method; Kontsevich & Tyler, 1999) was given an initial PSE estimate of 0° (no bias) with a standard deviation of 10° for that estimate, and an SD estimate of ±5° with a standard deviation of 10°. Each participant yielded a PSE and an SD score for each of the testing blocks.

For the control data, two one-way ANOVAs were performed on PSEs and SDs from the SVV (sharp), SHV and bimodal (sharp) blocks, to compare results to previous findings in Experiment 1. In addition, two mixed-model 2x3 ANOVAs were performed on PSEs and SD scores from the SVV (blurred), SHV and bimodal (blurred) in the control and vibration conditions. Because some participants did not complete both testing sessions, the "vibration" variable was treated as a between-subjects factor, for which the analysis uses a more conservative estimate of subject error. Three planned contrasts between the unimodal SDs and bimodal SDs were performed.

Additionally, 8 t-tests were performed to identify if a significant bias in PSE from 0° was present in each of the blocks; a Benjamini-Hochberg step-up FDR adjustment was made to correct for these 8 comparisons (Hochberg & Benjamini, 1990).

Finally the PSEs and SDs of the unimodal conditions (SVV sharp/blurred and SHV) were used to predict the statistically optimal PSE and SD scores for all three bimodal conditions, according to the formulas 4.1, 4.2 and 4.3 discussed above. These predicted scores were compared to raw data using paired t-tests.

4.3 Results

4.3.1 Point of Subjective Equivalence (PSE)

The mean PSEs for each condition indicate the perceived direction of gravitational vertical. Mean PSEs and standard errors are reported in Table 4.2. Mean PSEs from the SHV, SVV (blurred) and bimodal (blurred) in the vibration and no-vibration conditions are plotted with 95% confidence intervals in Figure 4.4.

A one-way ANOVA comparing PSE scores for SHV, SVV (sharp) and bimodal (sharp) found a significant main effect of modality, $F(2,30)=21.01$, $p<0.001$. SVV sharp and bimodal sharp PSEs showed a significant A effect, $t\ (15)=-3.26$, $p=0.005$ (SVV sharp) and $t\ (15)=-2.92$, $p=0.011$ (bimodal sharp). SHV did not statistically differ from 0°.

	PSEs				
	SHV	**SVV (sharp)**	**Bimodal (sharp)**	**SVV (blurred)**	**Bimodal (blurred)**
No vibration	2.0 ± 1.0	-2.6* ± 0.8	-3.0* ± 1.0	2.7* ± 1.0	2.6* ± 0.9
			-2.1 ± 0.8		*2.3 ± 0.8*
Vibration	6.4* ± 1.4	-	-	2.5* ± 1.1	2.7* ± 0.9
					4.3 ± 1.1

Table 4.2. Means and standard errors (in degrees) of PSEs for each test condition. MLE predicted values and standard errors for the bimodal conditions are shown in italics below raw scores. The * indicates a raw mean significantly different than 0°, or true gravitational vertical at $p<0.05$.

A mixed model ANOVA comparing SHV, SVV (blurred) and bimodal (blurred) found a significant modality x vibration interaction, $F(2,60)=6.41$, $p=0.003$. From Figure 4.4 it is clear that the addition of vibration significantly impacted PSEs for the SHV task, but not the other two tasks. There was also a main effect of modality, $F(2,60)=3.14$, $p=0.05$. There was no significant main effect of vibration. An independent t-test between SHV (vibration) and SHV (no vibration) found a significant difference between PSEs in these conditions, $t\,(1,30) = 2.64$, $p=0.013$. A t-test (controlled for by FDR) found the SHV (vibration) PSE was significantly different than 0° (true vertical), $t\,(15) = 2.64$, $p=0.013$. Neck vibration induced a strong E-effect in SHV, but did not appear to affect the other tasks (see Figure 4.5).

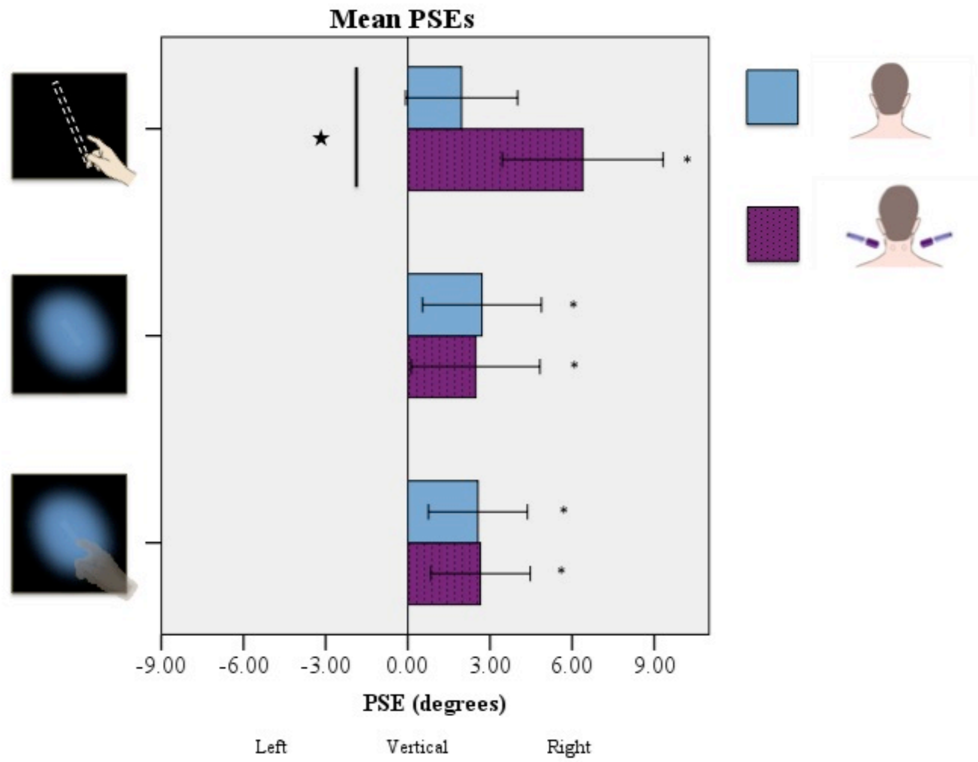


Figure 4.4. PSE scores obtained in the SHV, SVV (blurred) and bimodal (blurred) conditions, with or without applied vibration. Bars indicate 95% confidence intervals. An * indicates a PSE significantly different from 0°, or true gravitational vertical at p<0.05. The ★ indicates a significant difference between a pair of scores at p<0.05.

A curious finding was that the blurred visual rod induced a bias in PSEs *opposite* to the A-effect created by the sharply visible rod. Both SVV (blurred) and bimodal (blurred) showed a significant E-effect (bias opposite body tilt) in both vibration and non-vibration conditions: t (15) = 2.52, p=0.04 (SVV blur + vibration); t (15) = 3.11, p=0.007 (bimodal blur + vibration); t (15) = 2.66, p=0.018 (SVV blur + no vibration); and t (15) = 3.02, p=0.009 (bimodal blur + no vibration). SVV sharp and SVV blurred PSEs from the no-vibration condition are shown in Figure 4.5. A paired-samples t-test found these scores to be significantly different, t (15)= -4.16, p=0.001. The cause of this bias reversal will be discussed below.

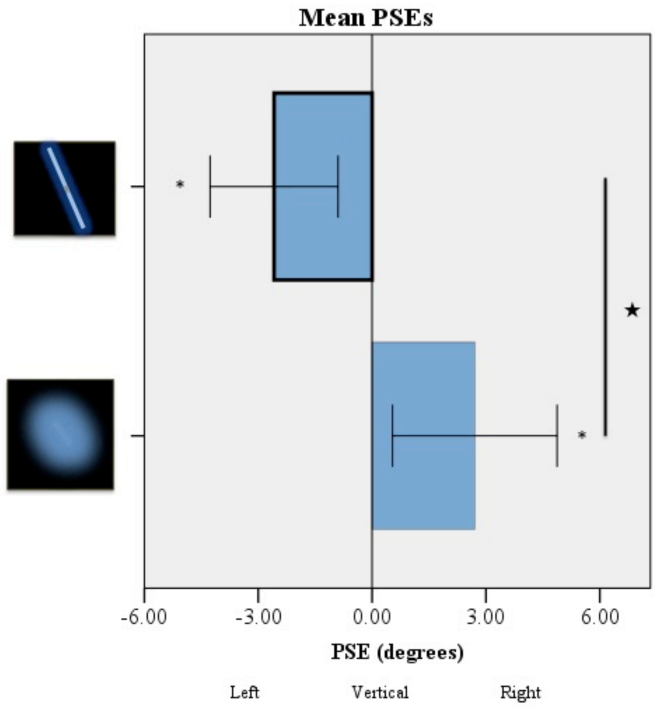


Figure 4.5. PSE scores of SVV (sharp) and SVV (blurred) in the no-vibration condition. Bars indicate 95% confidence intervals. An * indicates a PSE significantly different from 0°, or true gravitational vertical at p<0.05. The ★ indicates a significant difference between a pair of scores at p<0.05. Blurring the visual stimulus appears to significantly reverse the A-effect into an E-effect.

4.3.2 Standard Deviation (SDs)

In contrast to the PSE, which measures biases in perception, the standard deviation of the psychometric slope generated in each task is a measure of the *precision* of a given participant's responses. The reliability or precision of a cue is expressed as $1/SD^2$, where SD^2 is the variance of responses. The psi-method is optimized to measure the SD of participants' underlying psychometric functions for each of my experimental conditions.

Mean SDs for each condition are shown in Table 4.3 along with standard errors, and are plotted with 95% confidence intervals in Figure 4.6.

	SDs (degrees)				
	SHV	**SVV (sharp)**	**Bimodal (sharp)**	**SVV (blurred)**	**Bimodal (blurred)**
No vibration	5.7 ± 0.5	1.5 ± 0.1	1.9 ± 0.2 *1.4 ± 0.08*	3.9 ± 0.4	3.7 ± 0.3 *2.9 ± 0.2*
Vibration	5.3 ± 0.6	-	-	4.7 ± 0.5	2.9 ± 0.2 *3.3 ± 0.3*

Table 4.3. Means and standard errors (in degrees) of SDs for each of the tested conditions in Experiment 3. MLE predicted values and standard errors for the bimodal conditions are shown in italics below raw scores.

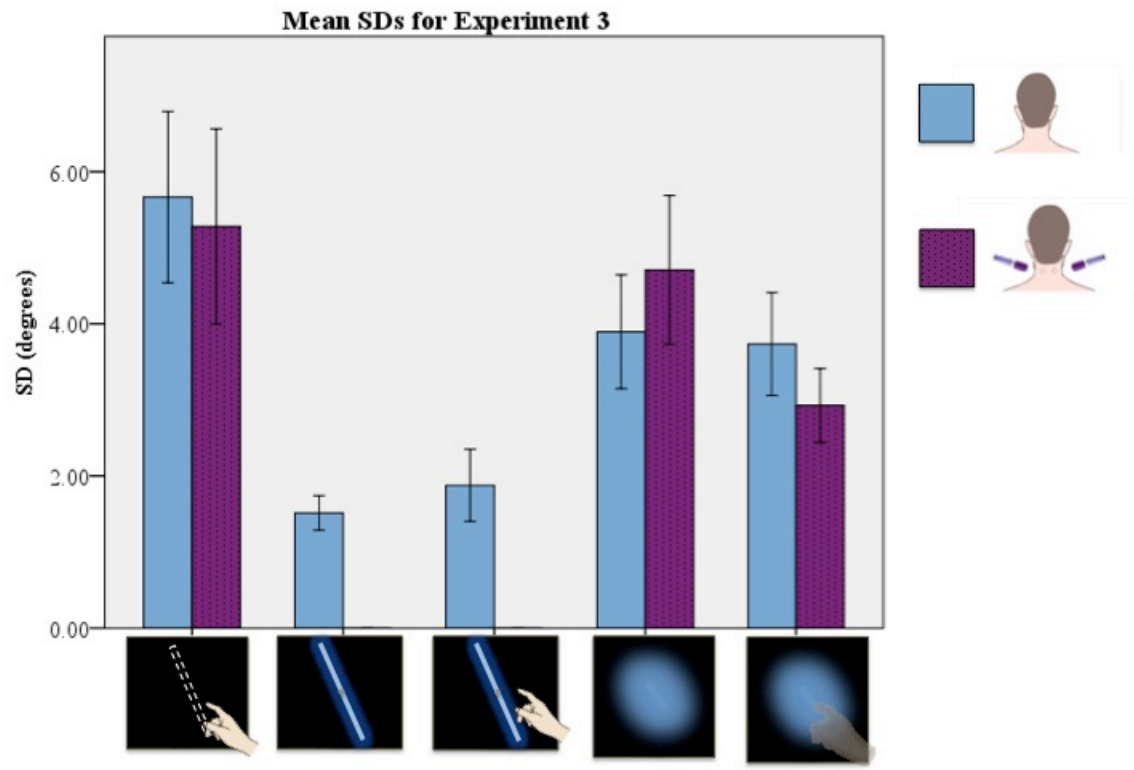


Figure 4.6. SD scores obtained in all tested conditions, with (purple) or without (blue) applied vibration. Error bars indicate 95% confidence intervals. The sharp-rod conditions were not run with neck vibration.

A repeated-measures ANOVA found a main effect of modality on precision, $F(2,30)=52.95$, $p<0.001$. Figure 4.6 shows that the SHV is a much less precise (larger SDs) measure than SVV (sharp) or bimodal (sharp). This difference in reliability between SVV and SHV has implications for optimal integration, which will be discussed below.

A mixed-model ANOVA comparing the SDs for the SHV, SVV (blurred) and bimodal (blurred) found a main effect of modality on SDs $F(2,60)=14.40$, $p<0.001$, but no significant main effect of vibration and no significant interaction. Thus while applying vibration significantly shifted mean PSEs it did not significantly affect overall precision of responses.

Planned contrasts showed that bimodal SDs were lower than average unimodal SDs for all conditions, t (15) = 6.47, p<0.001 (sharp stimulus + no vibration), t (15) = 2.60, p=0.020 (blurred stimulus + no vibration), and t (15) = 6.62, p<0.001 (blurred stimulus + vibration), indicating some integration of cues occurred, though as I show below only the bimodal (blurred + vibration) condition shows evidence of optimal integration according to Figure 4.3.

4.3.3 Optimal Integration – Comparing Bimodal PSEs and SDs to MLE predicted scores

The SDs and PSEs of the unimodal conditions were used to predict PSEs and SDs for each participant for the bimodal tasks, according to MLE using equations 4.1, 4.2 and 4.3 given in section 4.1. These are the scores we would anticipate if the visual and haptic cues were optimally integrated. Raw and predicted scores for PSEs and SDs are shown below in Figures 4.7 (PSEs) and 4.8 (SDs).

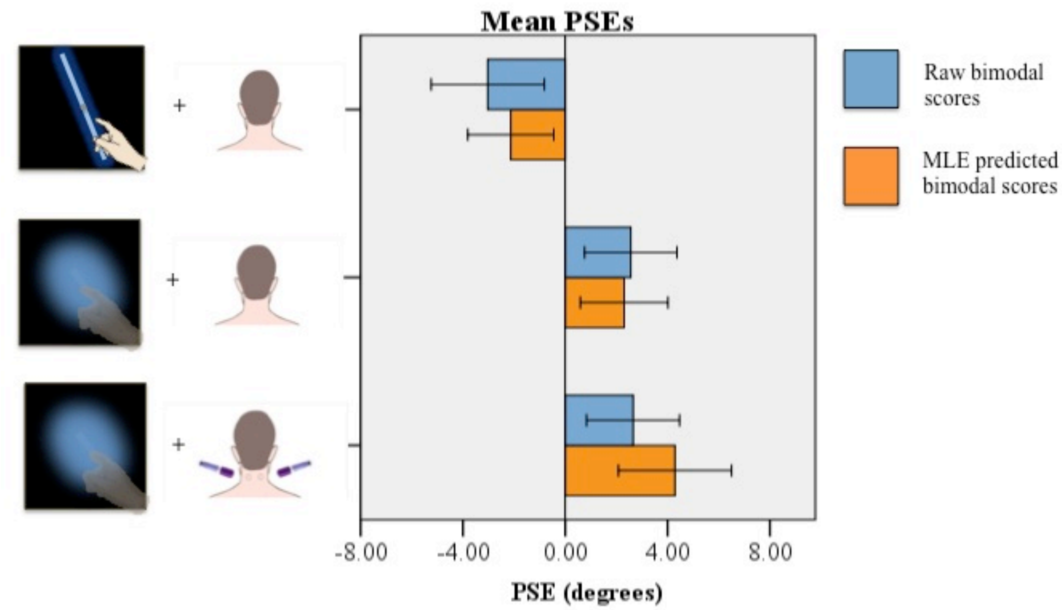


Figure 4.7. Raw and MLE-predicted bimodal PSE scores for all 3 bimodal conditions.

PSEs

The use of a sharp visual stimulus resulted in much greater precision than the haptic cue in the unimodal conditions. This implies that the sharp visual information is much more *reliable* than haptic information, and we would therefore expect visual information to be heavily weighted if the two were integrated optimally (see section 4.1). Under MLE, the PSE for two integrated sensory inputs is the average of each unimodal PSE weighted by their reliabilities. Thus we would expect a bimodal PSE with a heavily weighted visual component to skew towards the SVV (sharp) PSE, which it does (see Fig 4.4). Conversely, the blurred visual stimulus is less reliable (with comparable level of reliability to haptic information), and so we would expect a bimodal (blurred) PSE would be closer to an equally weighted average of visual and haptic components. I used paired t-tests to determine whether the raw bimodal scores significantly differed from the MLE model's predictions as a way to test the model's fit. Raw bimodal PSE scores did not differ from predicted scores in any condition, suggesting that bimodal responses are well accounted for by optimal integration of unimodal cues.

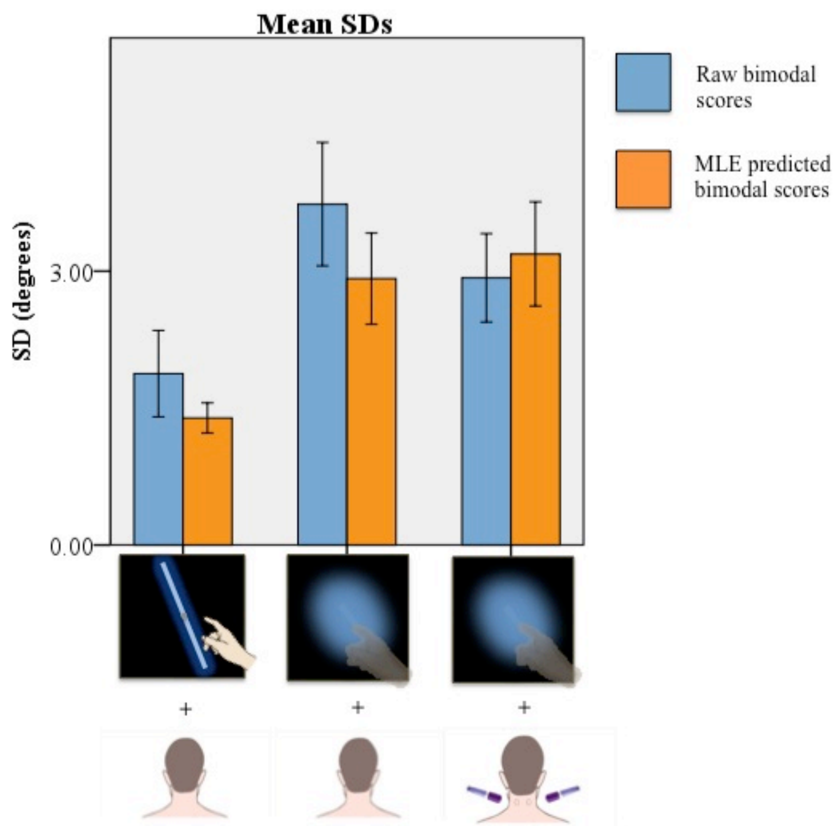


Figure 4.8. Raw and MLE predicted bimodal SD scores for all 3 bimodal conditions.

SDs

The MLE model also predicts that the precision, or reliability, of a bimodal cue will be greater that either of the contributing cues in isolation (see section 4.1). Thus I expect that the SDs of the bimodal conditions would be smaller than those obtained in the tested unimodal conditions. I used paired one-sided t-tests to determine how the estimated precision of the three bimodal measures compared to the precision predicted by the MLE model (one-sided, as our null hypothesis states that raw precision is no worse than optimal). Both bimodal (sharp) and bimodal (blur) SD scores were significantly greater than those predicted by the model, $t(15)=2.53$, $p=0.013$ (bimodal sharp) and $t(15)=2.30$, $p=0.018$ (bimodal blur). It thus appears the bimodal estimates are not as precise as we would expect if optimal integration of unimodal cues had occurred. In fact, post-hoc t-tests (corrected with FDR) confirmed that bimodal (sharp) SDs were no different than visual-only (sharp) SDs, ($p=0.059$), confirming visual dominance. Bimodal (blur) SDs were significantly better than visual-only (blur) SDs, $t(15)=4.74$, $p<0.001$, again suggesting some integration of visual and haptic cues occurred, though it was not optimal. Adding vibration to the bimodal (blur) condition resulted in SDs that did not significantly differ from the model's predictions ($p=0.17$), suggesting that adding noise to the neck afferents facilitates optimal integration of haptic and visual cues to verticality, and reduces the variability of the combined estimate to a level unlikely if there were a single underlying representation of gravity vertical. I argue that this integration is the result of the degradation of the indirect pathway, effectively decoupling of head and body reference frames.

4.4 Discussion

The goal of this experiment was to determine whether SVV and SHV access a single underlying gravity estimate, or two distinct estimates that share information. To measure this, I looked at a bimodal probe of verticality from the perspective of optimal integration. Two inputs will not optimally combine according to formula 4.2 and 4.3 if their sensory noise is highly correlated (i.e., they share a common source of noise). Thus a lack of optimal integration of SVV and SHV is compatible with the two probes accessing a common gravity estimate. Alternatively, optimal integration would suggest that SVV and SHV have access to independent measures of gravity vertical.

4.4.1 Evidence for two representations of gravity

Bimodal probes using sharp and blurry visual stimuli showed suboptimal cue integration (significantly worse precision than predicted by MLE and no advantage provided by touching the rod at the same time), compatible with a common source of noise. However, in the presence of neck vibration that disrupted proprioceptive information concerning the head's position on the body, the bimodal probe showed optimal integration, compatible with degrading the sharing cues to gravity and body-based cues and providing evidence that SVV and SHV may access different egocentric estimates of gravity vertical. The results supports the model proposed by Clemens and colleagues, that there are two egocentric estimates of gravity vertical that share gravity cues via proprioceptive information about the neck. Based on the results of Chapter 3, it seems likely that SVV preferentially accesses the estimate based on the head's position in space, while SHV accesses the estimate based on body position.

Why might two separate but interactive egocentric representations of gravity exist? It may be due to a natural division in sensory cues as restricted to the head (vestibular system) or largely the body (somatosensation, somatic graviception) (see Chapter 1). Barra and colleagues (2010) also highlight a corollary division in cortical pathways: thalamoparietal projections appear to be involved in somesthetic graviception, while thalamo-insular projections play a role in vestibular graviception.

4.4.2 Comparison to previous research

PSEs from the SHV, SVV (sharp) and bimodal (sharp) conditions in session 1 (no vibration) are plotted with 95% confidence intervals in Figure 4.9 alongside PSEs obtained from the -45° body tilt condition in Experiment 1 (see Chapter 2).

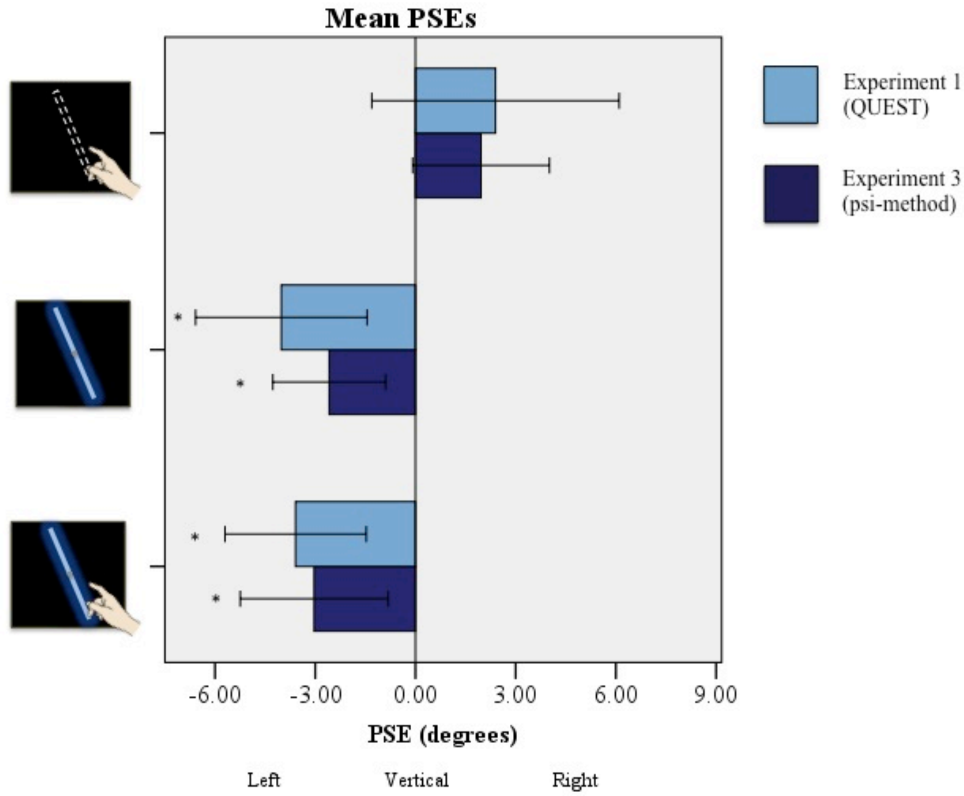


Figure 4.9. Comparison of PSE scores obtained in the SHV, and SVV and bimodal tasks where the stimulus is sharply visible in experiments 1 and 3. The experiments used a QUEST adaptive staircase or a psi-method algorithm to estimate PSEs. Error bars are 95% confidence intervals. An * indicates a PSE score significantly different than 0°, or true gravitational vertical, at $p<0.05$.

Experiments 1 and 2 used a QUEST adaptive staircase to identify PSE scores in the SHV and SVV and bimodal tasks while the stimulus was clearly visible. Experiment 3 (current chapter) used a psi-method algorithm to estimate PSEs as well as accurate SDs for each task (QUEST also generates SD scores, but these are not very reliable). Figure 4.9 compares results of SHV, SVV (sharp) and the bimodal (sharp) task using both staircases. Figure 4.10 compares staircases for an SVV trial in experiment 1 (QUEST) and this experiment (psi).

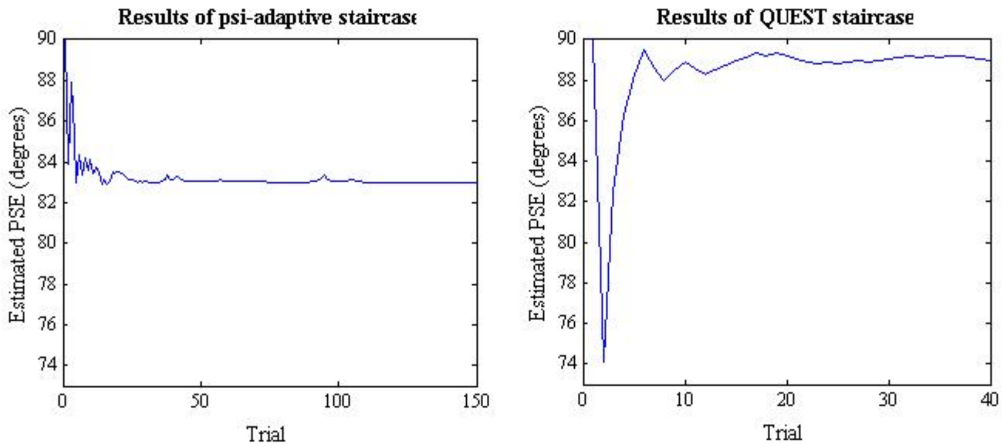


Figure 3.10 Comparison of results of two participants' psi and QUEST staircases on an SVV trial in this experiment (psi; left column) and experiment 1 (QUEST; right column). The x axis plots the trial number and the y axis shows the estimated PSE on that trial (note that QUEST uses this value as its next test angle; psi tests the shoulders of an estimated psychometric function and calculates this value indirectly). In the original code 90° indicated true gravitational vertical, and smaller values indicated a leftward tilt. These values were subsequently converted for statistical purposes.

A mixed model ANOVA (modality x testing method) shows a main effect of modality, $F(1,30)=31.63$, $p<0.001$ but no effect of test method ($p=0.67$) and no interaction ($p=0.62$). SVV sharp and bimodal sharp PSEs both showed a significant A effect, while SHV did not statistically differ from 0°. Thus Experiment 3 also replicated the biases reported in Experiment 1. From the perspective of PSEs, QUEST and the psi-method appear to be comparable.

4.4.3 Sharp vs. blurry: a reversal of SVV errors?

A surprising finding of this experiment was that a clearly visible rod evoked an SVV bias towards the body tilt, and a blurred, degraded stimulus evoked a bias away from the tilt. Why might specific stimulus characteristics promote different errors in visual verticality perception? Wade (1969) and Luyat and colleagues (2012) tested SVV using different test line sizes and found that larger lines elicited an A effect, while shorter lines evoked an E effect, consistent with our findings (Luyat and colleagues used two lines, one spanning 18.95° of visual angle, the other at 0.95°. By contrast the visual angles I used were roughly 37°, and 7° with blur). Luyat and colleagues suggest that this reversal of error may be due to the additional eye movements evoked by a larger stimulus (one expanding into the periphery) creating additional cortical activation. This would be an interesting premise for future imaging and eye tracking studies.

4.4.4 Neck proprioception and SHV

Another surprising finding was that decoupling the head-based cues to gravity from the body-based gravity estimate via neck vibration generated profound E effects in SHV, similar to those found in Experiment 2 when the vestibular system was disrupted. This implies that while the SHV seems to access a body-based gravity estimate, it is the indirect pathway that provides the most *accurate* estimate of gravity vertical for SHV. In all situations where this pathway is degraded, SHV estimates are heavily skewed away from the direction of tilt. Bauermeister and colleagues (1964) showed that the SHV E effect shifts in the direction of the hand used (e.g., right-handed estimates are shifted to the right, and left-handed to the left, with bimanual estimates in between). The authors used an adjustment method compared to the FR method I used here, but it is nonetheless possible that part of the rightward skew in my results was the use of the right hand in all measures. Further experiment using both left and right hands and left and right tilts could clarify this issue.

4.4.5 Summary

Visual and haptic measures of verticality (i.e., the perceived alignment of an object with gravity vertical) appear to access two different underlying representations of gravity vertical. Based on previous research these two representations of gravity vertical are thought to be head-based (SVV), and body-based (SHV). I argue the two estimates can be dissociated by vibration of the neck afferents, which decouples shared information and permits optimal integration of SVV and SHV. The diverging errors in SVV and SHV may be due in part to these separate gravity estimates and their relative contribution to each measure when coupled, but our data also suggest that stimulus characteristics (e.g., a sharply visible versus blurry rod) may contribute to these errors.

CHAPTER 5: General Discussion

The question posed at the beginning of my thesis was, do SVV and SHV probe the same estimate of gravitational upright? The answer is predominantly no. Properties that suggest the SVV and SHV are different include the fact that they show divergent errors as the body roll-tilt increases (Experiment 1), and are differentially affected by body-only tilt, head-only tilt, and potentially vestibular noise (Experiment 2). Furthermore, the two measures seem to rely on different representations of gravity vertical, with the SVV depending more on head orientation and the SHV depending more on body orientation. However, there is evidence that these two gravity estimates are linked by shared information concerning the position of the head on the body (Experiment 3). Thus, while SVV and SHV appear to make use of gravity estimates in different coordinate systems (Clemens and colleagues' two frame model, 2011), they also share properties as a result of sharing positional information between them.

SVV and SHV errors reported in the literature vary, in part due to differences in experimental procedure and the use of the adjustment method, which is sensitive to hysteresis and response artifacts (Tarnutzer at al., 2012b, Baccini et al., 2013). In Experiment 1, I compared SVV and SHV using a forced-response methodology in an attempt to minimize these potential confounds. I found that within the same subjects, SVV and SHV diverged as magnitude of whole-body roll tilt increased. SVV trended towards an A effect (bias towards tilt) which became significant at 45° of tilt. In contrast, SHV trended towards an E effect (bias opposite tilt) but did not reach significance. A novel bimodal probe I also tested showed dominance of the visual cue when both haptic and visual cues were available.

The difference in results of the two measures might stem from differences in the underlying gravity estimates they access, or by a modality-specific “idiotropic” prior (as Schuler et al., 2010 suggested that the prior might only affect visual judgments, see section 1.4). In Experiment 2 I addressed these possibilities by 1) manipulating the tilt of the head and the body relative to gravity separately and measuring SVV and SHV, to determine whether contributions of the head and body were weighted differently in the two tasks, and 2) using GVS to generate vestibular noise that might lead to a heavier weighting of a vision-specific prior. Results showed a differential weighting of body parts to SVV and SHV errors (both head and body tilt prompted SVV A effects, while only body tilt evoked an SHV A effect). The vestibular noise appeared to *suppress* all three of these errors, and induced a large E effect for SHV in the head-only tilt condition, which was previously accurate; though it is possible these results were due to vestibular noise shifting all estimates to the right. Given these results, it is unclear whether an idiotropic vector of the sort proposed by Mittelstaedt (1983) and further described by MacNeilage et al., (2007) is in fact the source of errors in visually perceived verticality.

Finally, in Experiment 3 I sought to identify whether the differential weighting of head and body parts in SVV and SHV reflected a difference in the underlying representations of gravity accessed by both tasks. Using Clemens’ et al’s (2011) two-frame model of gravity perception as a framework (see figure 4.1), I hypothesized that if SVV and SHV used different gravity estimates then it was feasible that the two cues would optimally integrate in accordance with the Maximum Likelihood Estimate (see section 4.1.2). In contrast, if the two shared a single underlying gravity estimate, then the two measures would shared positively correlated sensory noise, and a combined-cue measure should show significantly reduced precision compared to an optimal model. In order to test this I created two levels of a visual probe (sharp & blurry) and tested unimodal SVVs, unimodal SHV and two subjective bimodal verticals (SHV + sharp & SHV + blurry). In addition I created a novel manipulation in which I used bilateral upper dorsal neck vibration to disrupt neck afferents and effectively "decouple" head- and body-based estimates of gravity vertical, and then tested unimodal SVV (blurry), SHV and bimodal vertical (SHV + blurry). Results showed that when neck afferents were reliable, integration of visual and haptic verticals resulted in bimodal precision that was significantly worse than would be predicted if the two measures were independent. When vibration was applied, however, integration was optimal.

These results, along with those from Experiment 2, indicate that SVV seems to access a head-based representation of gravity vertical, while SHV access a body-based representation. These two estimates of gravity vertical are not wholly distinct, as sensory information can be shared between the two via perceived knowledge of the head's position on the body (i.e., neck afferents). SVV has been used as a clinical diagnostic tool for measuring vestibular function (e.g., Anastasopoulos et al., 1997; Vibert et al., 1999). The findings of my research highlight a distinct but complementary role for SHV in testing somatograviceptive function.

It was my hope that in the course of comparing SVV and SHV, I might come to elucidate the source of the unique pattern of errors in the two tasks when the body is roll-tilted. In Experiment 2, I found no evidence for the influence of an idiotropic prior for SVV, and in Experiment 3, I found that shortening and blurring the visual stimulus reversed the A effect to an E effect. This latter result potentially explains some of the variance in previously reported SVV errors. Taken together along with the results of Luyat et al., (2012) who showed a similar effect of line length, these results point to SVV errors being the result of misperception of the test stimulus, rather than of gravity vertical. The role of ocular torsion and eye movements in SVV errors merits further consideration in future studies.

SHV errors, in contrast, appear to be due to a complex interaction between perceived neck angle, body position and vestibular information. When the whole body is tilted 45° we see a trend towards an E effect that does not reach significance (Experiments 1 and 3). When it is only the body tilted 45° and the head is upright, this becomes an A effect, although it is suppressed by additional vestibular noise (Experiment 2). Curiously, when the head is tilted and vestibular noise is added (Experiment 2), or when the whole body is tilted and neck vibration is applied (Experiment 3), we see a profound E effect emerge. These results are hard to reconcile; what is clear is that SHV relies on vestibular information to inform its verticality estimate. Some of these biases I observed might be the result of how this vestibular signal is interpreted in body coordinates depending on the position of the neck. One possibility is that there is some default bias in perceived body orientation that is corrected by vestibular input; in the absence of this input (either due to GVS, decoupling by neck vibration or the suboptimal performance of otoliths at head tilts away from vertical), this default may come to dominate the SHV. Another possibility is that there is a bias in the proprioceptive information about neck position that leads to systematic overestimation or underestimation of the body's position based on the orientation of the head. A future study will examine these two possibilities and attempt to dissociate them experimentally.

One of the major limitations to these experiments was that only a small range of roll-tilts was tested. Kaptein and Van Gisbergen (2004) and Bauermeister et al., (1964) show that at very large roll tilts SVV and SHV patterns can sometimes reverse, which would be worthwhile testing under GVS and neck vibration conditions. In addition, my use of the FR method to test SHV has not been compared experimentally to the adjustment technique; the two tasks may not be comparable, which makes it difficult to compare my findings to previous SHV research. A future study will directly compare the ADJ and FR methodologies in SHV, in a manner similar to what Baccini and colleagues (2013) did for SVV. Finally, it would be worthwhile in future experiments to collect more participant data on the subjective experience of GVS and neck vibration, in the hope of qualifying these measures better, so that they might become better understood scientific and clinical tools.

The perception of gravity is invaluable for our daily life, and yet in a consideration of the bodily senses it is often overlooked. The perception is so automatic and intuitive to us, that it seems hardly a glamorous subject for scientific inquiry. Yet I hope that this thesis has illustrated that the perception of gravity is a complex, multifaceted and multisensory topic that, though humble, is worthwhile investigating. It is my hope that measures of gravity perception such as SVV and SHV will find new clinical and practical applications as the underlying nature of the two paradigms becomes better understood.

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Appendix: Consent Forms

Appendix A. Consent form used for experiments described in Chapters 2, 3 (controls) and 4

Informed Consent Form

Date: February 20, 2014
Study Name: Orientation Perception with Head and Body Misaligned

Researchers: *Laurence Harris, room 1022 Sherman Health Research Centre. X 66108 harris@yorku.ca*
Lindsey Fraser room 1022 Sherman Health Research Centre, lfraser4@yorku.ca
Bobbak Makooie room 1022 Sherman Health Research Centre

Purpose of the Research: To assess whether the perceived orientation of visual stimulus changes when either the head, the body or both head and body are tilted.

What You Will Be Asked to Do in the Research: You will either stand upright or lie inclined on a specially constructed wooden platform. This platform has been extensively used in previous experiments to support participants placed at a number of body orientations. Your head and body will be aligned upright, or inclined by various amounts between upright and horizontal and supported by a foam support. You may be asked to tilt your head while standing upright (supported by a foam support) or keep your head upright while lying on the platform (also supported). You may also be asked to wear a non-restrictive apparatus that will apply mild vibration to your lower neck during the experiment. In the experiment you will be asked to look at and/or touch a rod. You will be asked to make judgments about the orientation of the rod relative to gravity. Each condition will take between 10 and 30 minutes each after which there will be a short break. You may take breaks more frequently if desired. The data will be collected over either one or two data collection sessions lasting each lasting up to two hours. We will record your sex and age as well as hand dominance.

Risks and Discomforts: We do not foresee any risks or discomfort associated with your participation in the research.

Benefits of the Research and Benefits to You: None

Voluntary Participation: Your participation in this study is completely voluntary and you may choose to stop participating in our experiments at any time. Your decision not to volunteer will not influence the nature of the ongoing relationship you may have with the researchers or study staff or the nature of your relationship with York University either now, or in the future.

Withdrawal from the Study: You can stop participating in the study at any time, for any reason, if you so decide. Your decision to stop participating, or to refuse to answer particular questions, will not affect your relationship with the researchers, York University, or any other group associated with this project. In the event you withdraw from the study, all associated data collected will be immediately destroyed wherever possible.

Confidentiality: All information you supply during the research will be held in confidence and unless you specifically indicate your consent, your name will not appear in any report or publication of the research.

The data will be stored on a computer. Your data will be safely stored in a locked facility and only research staff will have access to this information. Your data will be destroyed when the study is complete. Confidentiality will be provided to the fullest extent possible by law.

Questions about the Research? If you have questions about the research in general or about your role in the study, please feel free to contact Dr. Harris either by telephone at 416-736-2100, extension 66108 or by e-mail (harris@yorku.ca). This research has been reviewed and approved by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, York Research Tower, York University (telephone 416-736-5914 or e-mail ore@yorku.ca).

Legal Rights and Signatures:

I________________________________consent to participate in *"Orientation Perception with Head and Body Misaligned"* conducted by Dr. Laurence Harris, Ms. Lindsey Fraser and Mr. Bobbak Makooie. I have understood the nature of this project and wish to participate. I am not waiving any of my legal rights by signing this form. My signature below indicates my consent.

Signature ______________________________ **Date** ______________________
Participant

Signature ______________________________ **Date** ______________________
Principal Investigator

Appendix B. Consent form used for experiment described in Chapter 3 (GVS condition)

Informed Consent Form

Date: January 2014

Study Name: Effects of galvanic vestibular stimulation on Judging Vertical During Head Tilt

Researchers: *Laurence Harris, 1022 Sherman Health Research Centre, x 66108, Lindsey Fraser, Bobbak Makooie*

Purpose of Research: To look at the accuracy and precision of subjective haptic and visual vertical while upright.

What You Will Be Asked to Do in the Research. You will perform two tasks where you are required to judge whether a rod is tilted with respect to gravity. Throughout the duration of this task galvanic vestibular stimulation (GVS) will be applied via electrodes placed behind your ears in intermittent bursts. The first task involves lying on a tilted board with your head cushioned so that it is upright, while in this position you will judge whether a rod is tilted with respect to gravity visually and by touch. The second task entails making the same judgments as in the first, but while standing with your head tilted. Note that our apparatus involves:

Risks and Discomforts: Your arm may get tired while doing the task. Multiple breaks will be offered.

Benefits of the Research and Benefits to You: None.

Voluntary Participation: Your participation in the study is completely voluntary and you may choose to stop participation at any time. Your decision not to volunteer will not influence the nature of the ongoing relationship you may have with the researchers or the nature of your relationship with York University either now, or in the future.

Withdrawal from the Study: You can stop participating at any time, for any reason, if you so decide. If you decide to stop participating, you will be eligible to receive the promised compensation for agreeing to be in the project. Your decision to stop participating, or to refuse to answer particular questions, will not affect your relationship with the researchers, York University, or any other group associated with this project. In the event you withdraw from the study, all associated data collected will be immediately destroyed whenever possible.

Confidentiality: All information you supply during the research will be held in confidence and unless you specifically indicate your consent, your name will not appear in any report or publication of the research. The data will be stored in a locked facility and only research staff will have access to this information. The data will be stored for up to 5 years and then deleted. Confidentiality will be provided to the fullest extent possible by the law.

Questions About the Research? If you have any questions about the research in general or about your role in the study, please feel free to contact Dr. Harris either by telephone at (416) 736 2100, extension 66108 or by email (harrus@yorku.ca). This research has been reviewed and approved by the Human Participants Review Sub-Committee, York Universities Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights asa participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, York Research Tower, York University (telephone 417-736-5914 or email ore@yorku.ca).

Legal Rights and Signatures:

I ___________________________ consent to participate in the study on judging visual and haptic vertical while upright conducted by Dr. Harris and colleagues. I have understood the nature of this project and wish to participate. I am not waiving any of my legal rights by signing this form. My signature below indicates my consent.

Signature ________________________________ **Date** ______________________

Signature of Researcher ________________________________ **Date** ______________________